Assessment of grassland ecosystem functioning: Carbon dioxide exchange and the dynamics of carbon and nutrient pools in temperate and Mediterranean grasslands

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By:

Heydar Mirzaei

Kermanshah, Iran

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1.1. Introduction

Recent predictions indicate that global temperatures are likely to increase by 1.1 to 6.4 °C between 1990 and 2100 due to climate change (IPCC, 2001). The increase in global temperatures will lead to rise in sea levels as a result of melting glaciers, changes in the amount and pattern of precipitation, and increases in the frequency and intensity of extreme weather events. These changes will result in shifts in agricultural yields, changes in summer stream flows, increased species extinction and increases in the distribution range of disease vectors, (IPCC, 2002). Rising temperatures, changing precipitation and rising atmospheric CO_2 concentrations will become major drivers of changes in plant diversity and loss in the 21st century. A recent modelling study of 1350 European plant species predicted that half of these species will become classified as 'vulnerable' or 'endangered' by the year 2080 due to rising temperatures and changes in precipitation (Thuiller et al., 2005; Soussana, 2007).

Projected temperature increases are attributed to increased anthropogenic greenhouse gas emissions, which lead to warming of the earth's surface and the lower atmosphere due to increased greenhouse effect. The main natural greenhouse gases are water vapour, carbon dioxide, methane and ozone, causing about 36-70%, 9-26%, 4-9% and 3-7% of the greenhouse effect respectively (Pearson, 2000). The atmospheric concentrations of carbon dioxide and methane have increased by 31% and 149%, respectively, above pre-industrial levels since 1750. This is considerably higher than at any other time during the last 420,000 years (Rees, 2005), the period for which reliable data is available, and calls for urgent attention to curb the escalation and to reduce the current figures.

Major increases in atmospheric CO_2 concentration are attributed to increased burning of the fossil fuels (Watson et al., 1996). However, natural ecosystem exchange of CO_2 also occurs and contributes significantly to global carbon budgets annually (IPP, 1996). The net carbon dioxide exchange by terrestrial ecosystems (NEE) will be affected by projected global warming, and by the increased incidence of extreme climatic events (Ciais et al., 2005). Grassland carbon (C) stocks and the role of grasslands as C sinks will become increasingly difficult to maintain in an altered climate and under high

atmospheric CO_2 concentrations, which may lead to saturation of the C sink in soils. It has been hypothesized that relatively small climatically induced changes in soil respiration (SR) could rival the annual fossil fuel loading of atmospheric CO_2 (Jenkinson et al., 1992; Raich & Schlesinger, 1992; Yuste et al., 2004). Land use change also contributes to increases in atmospheric CO_2 as a consequence of deforestation as well as grassland conversion, and cultivation of new arable land (Schimel et al., 2001). Arresting the escalation in atmospheric CO_2 levels requires that emissions into the atmosphere be significantly reduced and /or CO_2 withdrawal from the atmospheric pool must be stepped up. Plants, through carbon sequestration, play a significant role in regulating sinks of carbon, withdrawing the atmospheric CO_2 and converting it into assimilates and biomass during photosynthesis, translocation and storage (IPCC, 2000). Thus, natural ecosystems are now being studied with more interest, in order to establish their contribution to net atmospheric CO_2 exchange (Falge et al., 2002a). Most attention and long-term CO_2 flux research has been focused on forest ecosystems with a neglect of grassland ecosystems worldwide (Valentini et al., 2000; Baldocchi et al., 2001; Falge et al., 2001a). However, grasslands cover approximately 32 % of the total land area (Adams et al., 1990) and must play a significant role in balancing the global C budget (Batjes, 1998; Scurlock and Hall, 1998).

The global estimates of the relative amounts of C in different ecosystem types suggest that grasslands probably contribute 10-30% of the total biosphere store (Eswaran et al., 1993; Nosberger et al., 2000) and play an important role in the biosphere–atmosphere exchange of major greenhouse gases (GHG). Grasslands could also act as C sources (Ham and Knapp, 1998; Flanagan et al., 2002; Novick et al., 2004). The diversity, complexity and rapid dynamic changes in grassland ecosystems, however, make them difficult to characterize in terms of a general framework of their functioning. This is further complicated by the wide range of environmental conditions and management practices to which they are submitted. Further field studies are required, therefore, in order to understand the role of grasslands with respect to global climate change phenomena. This emphasizes a need to understand grassland ecosystem processes that relate to productivity, carbon exchange and nutrient dynamics in detail, as well as how they relate to environmental shifts and existing or potential future management practices.

In this study, attempts were made to elucidate some of the biophysical processes related to CO_2 exchange, biomass production and nutrient uptake and use in temperate and Mediterranean grassland ecosystems. Although the experiments were conducted in temperate grassland in Germany and the Mediterranean region of Portugal, the longer-term aim of this work is to extrapolate the results in future studies to the temperate and Mediterranean grassland ecosystems of Iran, which have similar climate and vegetation characteristics to those of the studied sites. Overgrazing, intensive land use, and extreme weather events due to climate change contribute to degradation of the natural grasslands in Iran. New concepts are required, in order to develop approaches aimed at optimizing their production and maintaining them as a sink for CO_2. Approaches evolving from this study could be replicated in similar temperate and Mediterranean grassland ecosystems of Iran in order to achieve the author's personal objectives of obtaining greater insight into the function of those systems. In the literature review, the Mediterranean and temperate grasslands of Iran are briefly mentioned as systems where similar objectives to those of the current study are extremely relevant.

1.2. Literature review

1.2.1. General overview of temperate and Mediterranean grasslands

1.2.1.1 Temperate grasslands

Temperate grasslands comprise approximately 32% of the earth's natural vegetation (Adams et al., 1990) and about 20% of the land area in Europe (Soussana et al., 2004). Except for Antarctica, they occur on all continents of the globe, including southeast Australia; the *pampas* of Argentina; the *prairie* and *plains* of North America; the *steppes* of eastern Europe, northern Eurasia and eastern Asia; and the *grassveld* of South Africa. These temperate grasslands represent one of the earth's major biomes, and historically at least, one of the most productive and diverse of all terrestrial ecosystem types (ICUN, 1999). The maintenance of high diversity in grasslands is dependent on management practices such as grazing, cutting and other manipulations, which in turn may have influences on soil fertility (Bakker, 1994; Berendse et al., 1994; Critchley et al., 2002). Some of these vegetation formations are natural, while others are anthropogenic in origin (Jones and Donnelly, 2004).

Temperate grassland vegetation is composed of a rich mix of grasses and forbs, and such ecosystems are underlain by some of the world's most fertile soils. They receive approximately 500 to 2000 mm of precipitation per year and temperatures range from -20 to 30°C. In areas where grasslands are the climax vegetation (e.g. the steppes of Central Asia and the natural prairies of North America), rainfall is low enough to prevent the growth of forests. Where grasslands are non-natural (e.g. northwestern and central Europe, New Zealand, parts of North and South America and Australia), rainfall is normally higher and the climax vegetation is forest. These climatic differences mean that the productivity of natural grasslands is generally low while that of the non-natural grasslands is significantly higher (cf. Li et al., 2008), with the result that they tend to be used more for intensive agricultural production (Whitehead, 1995).

Current global circulation models, predict an increase in temperatures of between 4 and 6°C for the regions of the world where temperate grasslands are now located (Mitchell et al., 1990). Combining the large surface area impacted and the expected magnitude of predicted climate change, changes in the carbon budgets of temperate grasslands should

have a significant influence on the earth's atmosphere. Intensively managed and fertilized temperate-region natural grassland ecosystems have extensive fibrous root systems and represent important C sinks in the global C budget (Rastetter et al., 1992; Frank, 2001; Hunt et al., 2002).

Environmental stresses resulting from climate change can substantially reduce plant production in temperate grasslands (Parton et al., 1994). Grasslands show the largest inter-annual variation in primary production (within grasslands) due to changes in precipitation. Productivity increases in wet years are much more pronounced than reductions in productivity during drought years (Knapp and Smith, 2001). Short-term studies have shown that temperate grasslands are sinks for atmospheric CO_2 during their peak biomass accumulation period, but annual data are limited (e g. Bruce et al., 1999; Conant et al., 2001; Jaksic et al., 2006). The results of a number of European research studies (see Frank, 2001; Soussana et al., 2007; Gilmanov et al., 2007) indicate that European temperate grasslands are currently acting overall as net sinks for atmospheric CO_2.

1.2.1.2. Mediterranean grasslands

Mediterranean ecosystems are characterized by mild, rainy winters and hot summers with high radiation and little or no precipitation. They are located at mid-latitude between 30 and 35° North and South in five distinct parts of the world; the Mediterranean Basin, California (U.S.A.) and Baja California, Mexico, central Chile, the Cape Province, South Africa, and southwestern Australia. More than three-quarters of the total Mediterranean-type ecosystems are distributed within the Mediterranean Basin. Mediterranean ecosystems occupy less than 5 % of the Earth's surface, yet they contain about 20 % of the world's flora (Cowling et al., 1996). Mediterranean type vegetation can range from forests to woodlands, shrublands, and grasslands. These regions are also recognised for their outstanding biodiversity (Cowling et al., 1996). In Europe, Mediterranean grasslands occur in Portugal, Spain, France and Italy, while in Asia, they cover the regions within the Mediterranean Basin, such as Turkey, Syria, Lebanon, Iran and Iraq. In North Africa, they are found in Tunisia, Algeria, Morocco and Egypt.

Mediterranean ecosystems are among the most heavily utilized by man and have been for long periods of time. Mediterranean regions are major centers of human population growth, and thus, anthropogenic impacts on natural ecosystems have been a matter of concern for centuries, particularly because of the potential for introducing new environmental problems or altering the frequency and intensity of existing ones (Mooney et al., 1986; Fuentes et al., 1990, 1995). As a result, Mediterranean ecosystems are frequently severely impacted. Because of these anthropogenic perturbations as well as strong ecological constraints such as long and dry summer, they are especially dependent on management practices compatible with the prevailing environment.

The Mediterranean climate is characterized by large seasonal and inter-annual variations in precipitation input (Mooney et al., 1974; Mooney, 1981; Pereira et al., 2007) and consequently, the length of the growing season and plant productivity depend on the beginning and the end of the rainy season. Mediterranean grasslands can be either net carbon sources or sinks depending on precipitation. More carbon uptake occurs during wet years and less during dry (Flanagan et al.; 2002, Meyers, 2001; Suyker et al., 2003). With shifting patterns of precipitation and increases in temperatures due to climate change, these ecosystems will shift in structure and function (Midgley et al., 2004).

Characteristics of the Mediterranean grassland ecosystems justify them as suitable models to study regional response to a variety of global change drivers and feedbacks to climate (Lavorel et al. 1998). Regions experiencing Mediterranean climate have highly specific rainfall patterns and changes in land cover and ecosystem physiology can potentially have a detectable impact on the regional physical climate. Mediterranean ecosystems are especially sensitive to climate change because of the transitional nature of this biome, which falls between temperate forest and desert. A small increase in the annual precipitation, for instance, can easily shift Mediterranean dryland communities toward low- cover desert shrubland with associated consequences for overall water and carbon fluxes (Owensby et al. 1996).

1.2.1.3. General eco-climatic zones of Iran: Similarities with the current study locations

Iran, with a total land area of 1,648,195 square kilometers lies between 25º 00′ and 39º 47′ N and 44º 02′ and 63º 20′ E. The southern half of the country has large areas experiencing Mediterranean type of climate. The northern half of the country is in the temperate zone. The mean altitude of the country is approximately 1,250 m above sea level. More than half of the country lies at altitudes of between 1,000 – 2,000 m. (Eivazi 1995). The northern temperate climate zones receive more than 1,000 mm of rain annually while the western and southern-west Mediterranean zones receive 480 mm of rainfall. The overall rainfall pattern is influenced by two major mountain chains. The Zagros Mountains are oriented along a northwest to southeast axis, and the Albors Mountains along the north toward the northeast. Moist clouds originating from the west are hindered by these mountains from reaching the central, eastern and southern parts of country, subjecting these regions to low precipitation (Badripour 2004). The great chains of Albors and Zagros form a "V shaped" natural barrier that inhibit penetration of moist air, and the majority of clouds coming from the north, southwest and south, from reaching the center of country. Consequently, large areas of steppe and deserts are found east of these mountain ranges. About 90 million hectare or 54.6% of the country is covered by temperate and Mediterranean grasslands and natural arid and semi-arid rangeland with a plant biodiversity of more than 8500 species.

1.2.1.3.1 Dominant grassland ecosystems of Iran

Steppe zone of Iran: This zone occurs in central Iran. Annual precipitation is between 100 –230 mm and temperature is highly variable according to altitude. The summer period is dominated by dry conditions. The steppe zone can be divided into three sub-zones on the basis of the mean winter temperatures; warm steppe, mild steppe and cold steppe, having; 10, 6, and 4°C mean annual temperature, respectively. Dwarf shrub vegetation (*Artemisia herbae-albae* i*ranica*) is common over large areas. Community species composition is very diverse and rich in non-saline areas, where many thorn-cushion species dominate ecosystem structure. Under extremely arid conditions, a very open variant of the dwarf shrublands occurs, characteristic of large areas of the Iranian

interior with the dominant species being *Astragalus spp* (ca. 800 species in the entire country; Frey and Probst, 1986). Many herbaceous species grow in this region, most of them being annuals, but in the mountains, perennials become abundant. Land area of this zone is about 49,500,000 hectare.

Sub-steppe zone of Iran: This zone forms a continuous strip around the Zagros Mountains to the southeast of the Albors Range and extends broadly into the northwest as well as west of the country. Annual precipitation is between 240 and 450 mm, temperature is variable especially in winter, depending on altitude and latitude. This zone, based on mean average winter temperature, can be further divided into warm, mild vs. cold sub-steppe zones. The sub-steppe flora is very rich in species, and has been strongly influenced by human activities. As far as dryland farming has been possible and where soils have not been eroded, the natural vegetation has been replaced or modified by weedy invasive species. Numerous invasive species originating in the steppe zone have spread into this zone. The herbaceous flora is much richer than in the steppe zone, well represented by individuals of the families *Compositae, Labiatae, Umbelliferae, Leguminosae, Caryophyllaceae, Crucifereae, Boraginaceae, Poaceae, Labiatae,* etc. Land area cover of this zone is 40,000,000 ha.

Mediterranean zone of Iran

This zone stretches along the Zagros chain, from south to northwest, and into the mountains in Azerbaijan. The altitude varies from roughly 800 to 2,600 m. Annual precipitation ranges between 450 to 800 mm depending on altitude. Temperatures vary from north to south, similarly influenced by altitude. Winters are mild on the southwestern border of the Zagros and cold or very cold elsewhere. The grassland and steppe forest areas of the Zagros Mountains have a semi-arid climate, (Anderson, 1999; Frey and Probst 1986). These grasslands are interspersed with oak trees that form canopies above the underlying herbaceous layer, similar to the Portuguese montado (Chapter 3). The dominant tree species found here include *Quercus persica, Q. infectoria, Q. libani and Pistacia atlantica.*. Dominant understory species are *Bromus tomentellus*, often associated with *Festuca valesiaca*, *F. ovina*, *Dactylis glomerata, Oryzopsis*

holciformis, Hordeum bulbosum, and many other useful species. Land area of this zone is about 18,000,000 ha.

1.2.1.4. Influence of environmental factors on grassland ecosystem functioning: emerging scenarios

Mediterranean grassland ecosystems

Fundamental changes in landscape structure (spatial and temporal) and functional attributes influence the spatial structure of plant canopies, species composition, physiology, nutrient availability and consequently biosphere-atmosphere gas exchange (Cernusca et al., 1998). Grassland ecosystem productivity and physiological processes are influenced by their environment as well as by management strategies. In Mediterranean grasslands, tree crowns strongly affect soil properties, diversity and productivity of the herbaceous layer under the trees. It has been theorized that trees and grasses are able to co-exist in Mediterranean ecosystems by occupying different niches, which can be separate in space or time (Eagleson, 1982; Rodriguez et al., 1999b; Baldoch et al., 2004).

Previous studies in the Mediterranean grasslands of Iran indicate that trees and shrubs have positive effects on their understory vegetation (Mirzaei et al., 1995). Improved microclimatic conditions as a result of the tree canopy lead to increased biomass and diversity of the herbaceous component under the trees as compared to open areas. Similar findings have been reported for other Mediterranean grasslands. Soils under tree crowns showed higher concentrations of organic matter, available N and other important nutrients, better physical structure, and faster water infiltration (Bernard and Reversat, 1982; Kellman, 1979; Tiedemann and Klemmedson, 1973). The herbaceous layer productivity was higher under large trees than under small trees and in open grasslands as a result of high soil fertility and increased soil water availability due to hydraulic lift (Fulco et al., 2004). Studies conducted in the Mediterranean ecosystems of southern Europe indicate more moist and nutrient-rich soils under the trees than in the open spaces (Joffre et al., 1988). Gallardo et al. (2000) reported that oak trees are a major source of temporal and spatial variability in the dehesa ecosystem of Spain, which is an extension of the Portuguese montado ecosystem. In their findings, they showed higher

concentrations of available nitrogen under the trees than in the open spaces between the trees. Similar observations have been reported for other ecosystems which share similar characteristics (Vetaas, 1992; Belsky et al., 1989 and 1993). Low radiation intensities, prolonged favorable microclimate, and improved nutrient status have been reported for areas under the trees in a tropical savanna, with a similar ecosystem structure (Belsky et al., 1989).

Such localized differences must profoundly influence the herbaceous layer dynamics, species distribution and the overall ecosystem productivity (Molofsky and Bever, 2002). Joffre and Rambal (1993) for example observed increased concentration of perennial grasses under trees while annual herbs were found in the open areas. Thus, quantification of ecosystem production demands the integration of productivity of the herbaceous layer under the tree canopies and in the open spaces between the trees that are subjected to higher radiation loads. Despite the crucial role played by the understory in the montado, few attempts have been made to systematically quantify its productivity, map out the structural dynamics, and un-code the underlying drivers of its high ecological diversity. There is little information on the role of ecosystem heterogeneity and diversity on carbon dioxide fluxes in Mediterranean grasslands.

Similarly, the effects of grazing on ecosystem processes that control C cycling and C distribution have not been sufficiently evaluated and documented for grassland ecosystems, including those of Iran. Since much of the grasslands of the world are grazed by domestic livestock, the effect of grazing on the carbon cycle of grassland ecosystems needs to be better understood (Daniel et al., 2002). For example, grazing reduced annual soil respiration by 18% in the US tall grass prairie (Bremer et al., 1998). In many ecosystems, grazing reduces aboveground and net primary productivity (ANPP), but there are examples where grazing actually increases ANPP (Milchunas and Lauenroth, 1993; Sims and Singh, 1978). McNaughton (1979) maintains that an optimal level of grazing will maximize ANPP in most rangeland ecosystems. Although the capacities of different ecosystems vary with respect to grazing, most of the reported negative effects of grazing relate only to specific ecosystems (Cain et al., 2002). Wallace (1990) indicated that there were increases in photosynthetic rate of big bluestem (*Andropogon gerardii*) under grazing, as compared to either clipped or control plants. Proper grazing

management has been estimated to increase soil C storage on US rangelands from 0.1 to 0.3 Mg C ha^{-1} $year^{-1}$, and new grasslands have been shown to store as much as 0.6 Mg C ha^{-1} $year^{-1}$ (Schuman et al., 2002). When CO_2 exchange rate (CER) was measured on sods from pastures with different stocking densities of sheep, it was found that a moderate stocking rate had higher (CER) than a light or heavy stocking rate (Vickery, 1972). In the mixed-grass prairie of Wyoming, USA, grazed pastures had higher community photosynthesis rates than ungrazed plots in the spring due to earlier "green-up" (LeCain et al., 2000).

In the natural grassland in New Zealand, nutrient decrease occurs on seasonally dry high country under grazing (Peter et al., 1997). Grazers impact the cycling of C and N within pastures via defoliation, excreta returns and mechanical disturbance. Information is lacking on the effects of grazing on CO_2 flux and soil nutrient properties in Mediterranean grasslands, yet pastoral system in these natural grasslands are more common than any other kinds of exploitation, and they must be taken into consideration.

Temperate grassland ecosystems

In temperate grasslands, which receive adequate precipitation throughout the year, the richness and composition of the plant assemblage remains important. The effects of plant diversity on ecosystem carbon flux have been reported in many studies, Naeem et al. (1994) reported a significant increase in community respiration at high compared to low and medium community diversity. The relation between plant species diversity and ecosystem CO_2 and water vapour fluxes was investigated for calcareous grassland communities, which in declining diversity significantly decreased ecosystem CO_2 assimilation in the first year of experimentation (Stocker et al., 1999). The average effect of a species on soil CO_2 flux was correlated with biomass of the species grown in monoculture (Craine et al., 2003), suggesting that effects of species on soil CO_2 flux are related to the potential productivity of a species and total belowground C allocation. During dry, warm conditions there is a greater effect of elevated atmospheric CO_2 on soil CO_2 flux and during these times deeper-rooted species contribute to soil CO_2 flux more than average. There is experimental evidence that aboveground productivity increases with increasing diversity (Stocker et al., 1999).

Usually, plants reduce photosynthetic capacity under drought (Reichstein et al., 2002; Aranda et al., 2005). However, higher carbon uptake into a grassland system is reported from Ireland during a dry year, although even the dry year did not pose severe water stress to the plants (Jasic et al., 2006). Furthermore, ecosystem respiration rates were reduced when rainfall was reduced by 50% in a Wyoming mixed-grass prairie (Chimner Walker, 2005). The interaction of diversity with climate may, therefore, play an important role in carbon assimilation and allocation as observed for functionally more diverse communities (Carine et al., 2001). Diversity has also been linked to ecosystem stability. The insurance hypothesis (Yachi and Loreau, 1999), states that communities which are more diverse in species or functional groups can be expected to be more resistant against environmental perturbations. Studies of CO_2 exchange in temperate grasslands with respect to community diversity need to be improved, especially in cases where they are influenced by extreme weather events. This can be undertaken with artificially structured grassland communities, and these will provide background information on the potential impact of climate change on natural ecosystems.

1.3. Statement of research problem

Ecosystem function refers to all the processes within an ecosystem through which the elements of the ecosystem change and interact. These processes are influenced by ecological, meteorological and anthropological factors. Thus, increases in temperature and shifts in precipitation (amounts and seasonal distribution) resulting from climate change may have significant impacts on natural ecosystems, particularly temperate and Mediterranean grasslands. Since they play an important role in the global CO_2 balance, understanding the structure and function of grasslands is essential to understanding their role in the global carbon budget. How they function, particularly in relation to CO_2 exchange and nutrient dynamics and how these processes are influenced by climate and management options is crucial in predicting the future of grasslands, as well as designing policies that will ensure sustainability, but also derivation of services for human well-being.

1.4. Objectives:

1. To determine how seasonal changes in microclimatic conditions influence soil water and nutrient availability, and their impacts on bioproductivity of temperate, Mediterranean and artificially created (concerning species composition) grasslands.
2. To explore the role of environmental stresses, ecosystem heterogeneity, species interactions and management methods in terms of their impact on CO_2 exchange, nutrient dynamics and productivity of temperate, Mediterranean and artificial grasslands.

1.5. Hypotheses:

1. The CO_2 exchange, nutrient dynamics and biomass production of European grasslands may be understood as the product of prevailing microclimatic conditions.
2. During periods with optimal climate conditions, CO_2 exchange, nutrient dynamics and biomass production of temperate, Mediterranean and artificial grasslands converge, i.e. exhibit the same characteristics.
3. An extremely simple light response model describing CO_2 gas exchange provides a tool that allows examination of similarities and differences in temperate, Mediterranean and artificial grasslands.
4. The differences in temperate, Mediterranean and artificial grasslands with respect to CO_2 exchange, nutrient dynamics and biomass production result from different temporal patterns in environmental stress.
5. Extreme weather events impose a stress on grasslands that alters CO_2 exchange, nutrient dynamics and biomass production.
6. Ecosystem heterogeneity resulting from species interactions significantly influences grassland functioning and productivity by altering microclimatic conditions.
7. Management methods have significant influences on grassland ecosystem functioning and its overall productivity.

Chapter 2
Material and Methods

2.1. Description of experimental sites

2.1.1. Temperate grassland

The experimental site was located in Grillenburg (50°57′04′′N, 13°30′51′′ E and 385 m a.s.l.), 13 km from the town of Tharandt and 28 km southwest of Dresden. The climate is characterised by a mean annual precipitation and air temperature of 760 mm and 8 °C respectively, based on 30 year average observations (1971-2000, Tharandt weather station). The site is usually covered with snow during December through February. The vegetation is dominated by the native fescue (*Festuca pratensis*), meadow foxtail (*Alopecurus pratensis*) and timothy (*Phleum pratense*). This temperate meadow is managed and maintained for periodic hay cutting with 2-3 cuts per year. The soils are described as wet Psuedo-gley (free from lime concretions up to the depth of 3 m), and are characterised predominantly by silty loam. The sand, silt and clay fractions in the top horizon (0-23 cm) and the next segment horizon (23-70 cm) are 10.3 %, 81.3% and 8.5% and 12.9%, 76% and 11.0%, respectively. The bulk densities of these two horizons are 1.4 and 1.7 g cm^{-3}, respectively.

2.1.2. Mediterranean grassland

The experimental site was located in the centre of the Alentejo Province, Portugal at Herdade da Mitra (38º 32' N, 8º 00' W, 243 m a.s.l) near the Mitra campus of the University of Evora, 150 km southeast of Lisbon. According to long-term averages (1951-1980), mean annual rainfall is 665 mm (90% of which falls from autumn to early spring) and mean annual open water evaporation is 1760 mm (INMG, 1991). Mean annual air temperature is 15 ºC, ranging from 8.6 ºC in January to 23.1 ºC in August. The summer period is from May until September and is characterized by dry weather conditions. The soil is a very shallow sandy Cambisol overlying a gneiss rock, with low soil water retention capacity (FAO, 1988). The grasslands occur within a woodland mosaic with the tree species *Quercus ilex* and *Quercus suber*. The understory in this mosaic consists in later successional stages of a mixture of shrubs dominated by *Cistus*

spp. With management, the understory is dominated by annual and perennial herbaceous species as listed in Table 2.1.

Tab.2.1. List of species collected at Herdade da Mitra, Portugal (Mediterranean grassland) during the growing season in 2006.

No.	Scientific name	Growth form	No.	Scientific name	Growth form
1	Anagallis monelli	F	34	Myosotis discolor	F
2	Anthemis fuscata	F	35	Narcissus bulbocodium	GL
3	Aphanes microcarpa	F	36	Ornithopus sativus	L
4	Aristolochia longa	F	37	Plantago coronopus	F
5	Arum italicum	F	38	Poa annua	G
6	Asparagus acutifolius	GL	39	Poa sp	G
7	Bellardia trixago	F	40	Quercus ilex (rotundifolia)	T
8	Bromus sp	G	41	Quercus suber	T
9	Calendula arvensis	F	42	Ranunculus aquatilis agg.	F
10	Callitriche spec.	F	43	Raphanus raphanistrum	F
11	Calycotome epineux	S	44	Rumex acetosella	F
12	Centranthus calcitrapae	F	45	Rumex bucephalophorus	F
13	Cerastium glomeratum	F	46	Rumex sp	F
14	Cistus crispus	S	47	Senecio aquaticus	F
15	Cistus salvifolius	S	48	Senecio lividus	F
16	Coleostephus myconis	F	49	Senecio vulgaris	F
17	Crassula tillaea	F	50	Sonchus oleraceus	F
18	Cynosurus echinatus	G	51	Spergula arvensis	F
19	Echium plantagineum	F	52	Stachys arvensis	F
20	Erodium romanum	F	53	Stellaria media	F
21	Fumaria agraria	F	54	Teesdalia nudicaulis	F
22	Galactites tomentosa	F	55	Trifolium dubium	L
23	Geranium molle	F	56	Tuberaria guttata	F
24	Geranium purpureum	F	57	Urginea maritima	GL
25	Iris sisyrhynchium	G	58	Veronica arvensis	F
26	Isoetes hystrix	GL	59	Vicia lathyroides	L
27	Juncus bufonius	G			
28	Lamium amplexicaule	F	**G= Grass**		
29	Leontodon taraxacoides	F	**F= Forb**		
30	Lotus corniculatus	L	**L= Legume**		
31	Medicago sp	L	**Gl= Grass like**		
32	Moenchia erecta	F	**S= Shrub**		
33	Montia minor	F	**T= Tree**		

2.1.3. Controlled garden experiments

Controlled experiments to investigate the effects of single extreme weather events on carbon balance of planted temperate grassland communities were conducted at the Botanical Garden of the University of Bayreuth in Germany (latitude 49°55'19''N, longitude 11°34'55''E and elevation 365 m asl). Bayreuth is influenced by temperate climate with mean annual temperature and precipitation of 7.8 °C and 709 mm respectively (German Weather Service). Annual precipitation is distributed bi-modally with the main peak during June/ July and a second peak during December/ January. The annual growing period starts at the end of March and aboveground biomass reaches its peak by early June with the growing season ending in late September or October.

2.2 Experimental design and observations

2.2.1. Temperate grassland

CO_2 flux data was obtained with manually operated closed chambers described in detail in section 2.3.1. These data were supplemented by information provided by the University of Dresden from an eddy covariance measurement tower (methodology summarized in the Appendix). Daily and seasonal courses of CO_2 exchange were graphically analyzed and related to changes in ecosystem structure and nutrient status. Biomass and soil nutrient properties were compared between an exclosure site within the area (protected from cutting) and the meadow which was mowed. Seasonal changes and treatments (cut and uncut) were examined to compare important parameters describing meadow gas exchange. The statistical analysis was performed using SPSS 14.

2.2.2. Mediterranean grassland

In order to evaluate effects of grazing and tree cover on CO_2 flux of herbaceous grassland vegetation, on above- and belowground biomass, and on nutrient content of soil, roots and the herbaceous layer, two adjacent locations, one fenced and the other unfenced were selected, representing grazed and ungrazed areas (Plate 1a). To represent the ungrazed area, vegetation was analyzed within a fenced exclosure where a hydrologic research station was located. The study site was protected against grazing and any disturbance since 1996 (David et al. 2006). In the two sets of treatments (sites), two sub-sites

comprising open (outside tree canopies) and shaded (understory) locations were studied, in order to examine the effects of trees on the herbaceous layer (cf. Plate 1b). The study was based on a factorial experimental design comprising grazing and shading as two main factors, and each factor consisting of 2 levels and 3 replications. Three campaigns were conducted during the study period, starting in March until May 2006, each campaign over a period of 10 to 14 days.

During a campaign, six plots in four combinations were selected randomly, and net ecosystem exchange (NEE) of CO_2 for the plots was measured using manually operated closed-system chambers from dawn to dusk over the course of a day (technical details given in section 2.3.1). The following paired comparisons were included in each campaign:

1. Grazed – shade plots versus grazed- open plots
2. Ungrazed –shade plots versus ungrazed –open plots
3. Grazed –shade plots versus ungrazed – shade plots
4. Grazed – open plots versus ungrazed –open plots

Aboveground biomass was harvested, and soil cores were extracted for determination of belowground biomass in individual plots after flux measurements were completed (see below).

Plate 1. (a) Adjacent ungrazed and grazed areas at Mitra, illustrating also the areas found in the open and below trees; and (b) an illustration of the existing vegetation mosaic with scattered oak trees that influence herbaceous vegetation structure and function.

2.2.3. Controlled garden experiments

To assess how changes in extreme microclimatic conditions and species composition will

potentially influence CO_2 exchange and productivity in temperate grasslands under global

change, a two-factorial experimental design was used manipulating (1) extreme weather events (drought, heavy rain in relation to control), and (2) community composition. The design consisted of 90 plots, each 2 by 2 m in size, with all factorial combinations replicated five times (cf. Jentsch, et al. 2007). Manipulations were applied in a modified Latin Square design; where experimental plant communities were blocked and randomly assigned within each manipulation. Original species composition was maintained by periodic weeding. Prior to the experiment, an area of 50 m by 70 m was prepared with homogenized substrate (about 80 cm in depth) where drainage facilitated to avoid soil related irregularities. Texture of the soil consisted of loamy sand (82% sand, 13% silt, 5% clay) with pH = 4.5 in the upper and pH = 6.2 in the lower soil layers (measured in 1M KCl).

The manipulations consisted of extreme drought, heavy rainfall in comparison to ambient conditions as a control. Intensity of the treatments was based on the local 100-year extreme event in each category. Vegetation periods (March to September) 1971-2000 were used as the reference period (German Weather Service). Gumbel I distributions were fitted to the annual extremes, and 100-year recurrence events were calculated (Gumbel, 1958). Accordingly, a drought period of 32 days and a rainfall extreme of 170 mm over 14 days were applied in the experiment during the peak growing season in June 2005. Maximum values in the historical data set were 33 days without rain during June and July 1976 and at the opposite extreme 152 mm of precipitation during 14 days in June 1977. Drought was simulated using rain-out shelters, constructed with a steel frame and covered with transparent plastic sheet that permitted nearly 90% penetration of photosynthetically active radiation. Near-surface air temperature was slightly, but not significantly, increased by the roofs during the manipulation period. Strong greenhouse effects are avoided by constructing the roof at 80 cm height, allowing for near-surface ventilation (Plate 2a).

Heavy rain was realized using portable irrigation systems (Plate 2b). Drop size and rainfall intensity resembled natural heavy rainfall events through application by Veejet 80100 nozzles, commonly used in erosion research (Kehl et al., 2005). The entire amount of added water was divided into two applications per day to ensure high soil water content, e.g., saturation. If natural precipitation occurred on treatment days, then the

amount of rain was subtracted from the required treatment dosage. Lateral flow water loss from the plots was avoided by use of plastic barriers around the treated plots.

Plant communities:

Overall, ten species were used during 2005 to establish artificial plant communities, which represent naturally occurring species combinations in German meadows. One hundred individuals per plot were planted in a systematic hexagonal grid with 20 cm distance between neighbors (Plate 3). Only two species combinations consisting of grasses or grass plus herbs were investigated in terms of ecosystem gas exchange as reported here:

1. Pure grass: community consisting of two grass species (*Arrhenatherum elatius* and *Holcus lanatus,* one functional group)

2. Mixed community: consisting of four grassland species *(Arrhenatherum elatius*, *Holcus lanatus*, *Plantago lanceolata*, and *Lotus corniculatus*, three functional groups - grasses, legumes and herbs)

Linear Mixed Effects Models were employed to test for weather manipulation and species diversity level effects while taking repeated measures into account (Faraway, 2006). First, the interaction between weather manipulations and diversity level with time as a random factor was assessed. If the interaction was not significant, the model was simplified to test only for weather manipulation effects by leaving out the interaction effect and using time (campaigns) and diversity level as random effects. Significance of differences ($p < 0.05$) was evaluated by Markov Chain Monte Carlo sampling of 1000 permutations (Bates and Campbell, 2001). The data was log transformed prior to statistical analysis, if conditions of normality were not met or if it was necessary to improve homogeneity of variances.

Both characteristics were tested by examining the residuals versus fitted plots and the normal qq-plots of the Mixed Models (Faraway, 2006). The statistical analysis was performed with the package lme4 (Bates and 3 Sarkar, 2007) in the computer language R (R Development Core Team, 2006).

Plate 2. Illustration of the experimental set-up for simulated extreme weather events, (a) drought treatment; and (b) heavy rain treatment in garden experiments during the early growing season in 2005

Plate 3. Illustration during the early spring of planted grassland communities at the University of Bayreuth. Apparent is the systematic hexagonal grid used for planting with 20 cm distance between neighboring individuals.

2.3. Measurements

2.3.1. CO_2 flux measurements with the chamber technique

2.3.1.1.Chamber description

Measurements of the daily course of net ecosystem CO_2 exchange (NEE) were carried out in the Botanical Garden of the University of Bayreuth (artificial temperate grassland), at Grillenburg (temperate meadow) and at Herdade da Mitra (Mediterranean grassland) using closed ecosystem chambers (Plate 4) from dawn to dusk over the course of the day. This technique was preferred because it relates to CO_2 flux estimation at plot scale, it is flexible for analyzing manipulation experiments, and it is accurate in comparisons with eddy covariance techniques (cf. Wohlfahrt et al., 2005; Li et al., 2008). Chamber measurements, therefore, permitted the evaluation of spatial variation in CO_2 fluxes that are dependent either on local habitat factors, due to herbaceous species composition or

due to management measures. At Grillenburg, data was also available from an eddy covariance tower operated by the University of Dresden (see the Appendix).

A portable closed chamber method (Plate 4a) described by Droesler (2005) was modified to estimate ecosystem CO_2 fluxes in the herbaceous vegetation. The instrumentation comprises two kinds of chambers of the same size; one transparent (from here on referred to as the light chamber) to measure NEE and the other one opaque (from here on referred to as dark chamber) to measure the ecosystem respiration (R_{eco}). The light chamber was constructed from a 3 mm thick Plexiglas XT type 20070. NEE is the net exchange including uptake by photosynthesis and loss by respiration, which can be represented as:

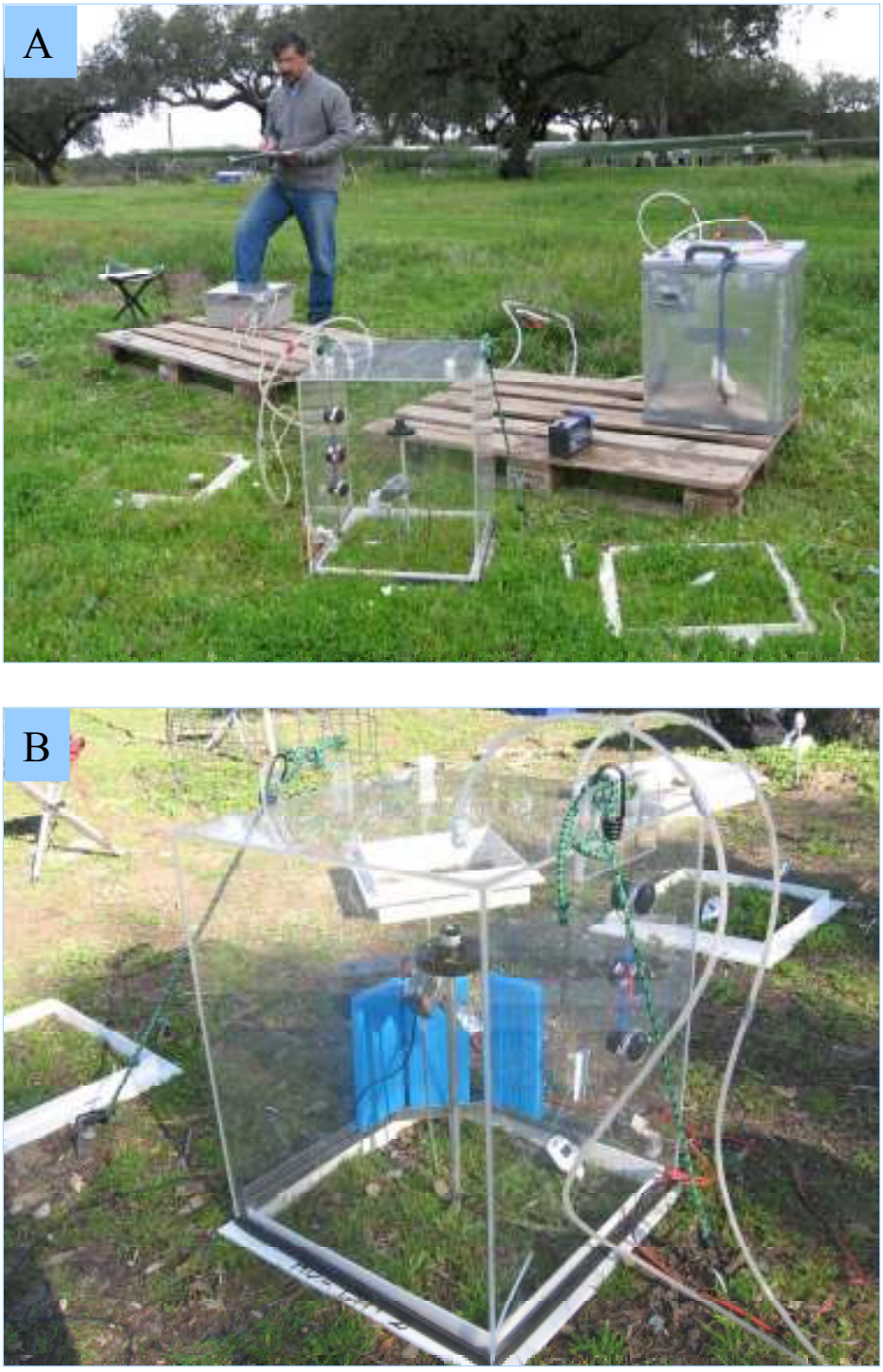
NEE = Photosynthesis – respiration

Ecosystem Respiration (R_{eco}) = $R_{plant} + R_{soil} + R_{roots}$

The base area of the chambers was 40 cm x 40 cm and the height was 54 cm. Depending on the height of the vegetation under consideration, the chamber height could be increased using open-ended extensions of different heights. These were available for both the light (transparent extensions) and the dark (opaque extensions) chambers.

Frost resistant collars with base area of 40 cm × 40 cm and 10 cm high, externally fitted with a 3 cm wide platform (3 cm from the top) were inserted approximately 7 cm into the soil, at least 3 days before measurements (cf. Plate 5). The chambers were fitted with a 2 cm diameter rubber material (Sahlberg, Germany) at the bottom edge, which rests on the platform during the course of measurements, ensuring airtight closure. Elastic cords were used to secure the chamber onto the collars. Sudden rise in pressure within the chamber was avoided by having a 3 cm diameter vent at the top of the chambers. Air temperatures inside and outside the chambers were continuously monitored in order to obtain close to ambient conditions inside the chamber during the measurements. Air temperature and humidity within the chambers were controlled by varying the number of ice packs inside the chamber, located opposite to the side with insolation (for light chamber). Adjustable fans were used to blow air over the ice packs and also maintain air mixing inside the chamber (Plate 4b). Soil temperatures at 5 cm depth and PAR conditions (in the light chambers) were monitored using soil thermometers and an LI-190 light sensor (Li-cor, Lincoln, Nebraska, USA). Approximately 95% of PAR were received inside the light

Plate 4. (a) The portable closed transparent chamber connected to an infra-red gas analyser as used for CO_2 flux measurement; and (b) a close-up illustrating the cooling and ventilation systems installed within the chamber.



chamber, while light intensity was reduced to zero inside the dark chamber. Flexible 0.318 cm diameter tubing (Bev-A-Line from LI-COR) was used to connect the chambers to an infra-red gas analyser (LI-800 or Li-820, LI-COR, Nebraska, USA). A battery-driven pump maintained flow of air through the chamber with closed air circulation at a constant rate of 1 l min^{-1} and with IRGA response time of 2.8 seconds. Each chamber was connected to a separate analyser during measurements. The analysers were calibrated every 3 days with the same CO_2 sources to ensure accuracy and compatability in measurements.

On each measurement day, CO_2 exchange over the vegetation was monitored from sunrise to sunset. Each round of measurements, depending on the numbers of the plots in the campaign, was different, lasting from approximately one half-hour to 1 hour. Experiments in the botanical garden in Bayreuth comprised 18 plots (two plant communities, three treatments and three replications), measurements in the montado included 6 plots (each site with three plots), and at the meadow in Grillenburg, 6 to 10 plots were included, depending on the campaign. On each plot, measurements lasted ca. 3 minutes before shifting to the next plot. Consecutive measurements were conducted with both dark and light chambers with the dark chamber lagging behind. Ecosystem CO_2 flux rates were calculated according to Equation 1.

$$F_{CO2} = k_{CO2}\,(273.15*T^{-1})(V*A^{-1})(p1*p0^{-1})(dc*dt^{-1}) \qquad \text{(Eq. 1)}$$

where:

k_{CO2} = gas constant at 273.15 K (0.536 µg C μl^{-1})

T = air temperature during the measurement (K)

V = total volume of the chamber, including extension

A = area of the collar (m^2)

p1 = pressure during the measurement (hPa)

P0 = 1013 hPa

$dc*dt^{-1}$ = rate of change in CO_2 concentration during the time of the measurement

After gas exchange measurements, the plots were used for biomass sampling. The aboveground biomass was measured by harvesting all plants within the 40 ×40 cm area enclosed within the frames.

Plate 5. Installation of soil frames 7-10 days before starting a measurement campaign in artificial grassland communities at the University of Bayreuth Botanical Garden.

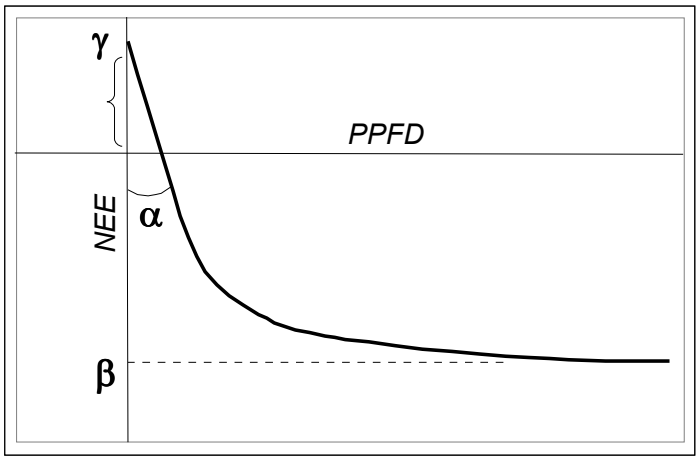
In Grillenburg the measurements were carried out during three campaigns within two sites (cut and uncut) in June, July and August 2004. CO_2 flux measurements in artificial communities at the botanical garden were carried out between June and September 2005. Three measurement campaigns within a 35 day time period were conducted. For each campaign, 18 chamber collars with 46 x 46 cm area were installed in two communities, three treatments and three replications about one week before starting flux measurements (Plate 5). In Mitra, six campaigns were carried out from the beginning of March until mid-May over the course of springtime, in order to develop a picture of the seasonal changes in CO_2 exchange occurring during this productive period, but results are reported here from three campaigns which focused on the grazed vs. ungrazed, and understory vs. open areas.

2.3.1.2. Estimation of model parameters describing gas exchange response

Empirical description of the measured NEE fluxes was accomplished via a non-linear least squares fit of the data to a hyperbolic light response model, also known as the Michaelis-Menten or rectangular hyperbola model (Fig. 2.1). This model inversion utilizes measured photosynthetically active radiation (PAR) and gas flux data from chamber experiments and provides **three fitted parameters**, α, β and γ. These parameters are estimated with NEE considered as dependent only on PAR (cf. Owen et al., 2007).

$$NEE = -\frac{\alpha * \beta * PAR}{\alpha * PAR + \beta} + \gamma \qquad \text{(Eq. 2)}$$

Fig. 2.1. Illustration of the relationship between the hyperbolic light response model used to describe NEE response, assuming only light as an independent variable, and derived parameters discussed in the text.



where NEE is net ecosystem CO_2 exchange (μmol CO_2 m^{-2} s^{-1}), α is the initial slope of the light response curve and an approximation of the canopy light utilization efficiency (μmol CO_2 m^{-2} s^{-1}/μmol photon m^{-2} s^{-1}), β is the maximum NEE of the canopy (e.g., uptake rate in μmol CO_2 m^{-2} s^{-1}), PAR is the photosynthetically active radiation flux (μmol photon m^{-2} s^{-1}),. γ is an estimate of the average ecosystem respiration (Reco)

occurring during the observation period (μmol CO_2 m^{-2} s^{-1}), (α/β) is the radiation required for half maximal uptake rate, and (β+γ) is the theoretical maximum uptake capacity. These parameters are fitted once for all selected data, then NEE is recalculated based on these fitted parameters and can be compared to observations to examine goodness of fit. Fitting for each plot, site and campaign individually, indicated that the coefficient of determination ranged from 0.85 to 0.95, when averaged over all plots (see results).

Since the rectangular hyperbola may saturate very slowly in terms of light, the term $\frac{\alpha * \beta * PAR}{\alpha * PAR + \beta}$ evaluated at a reasonable level of high light (e.g. PAR = 2000 μmol photons m^{-2} s^{-1}) approximates the maximum in gross primary production, GPP, and can be thought of as the average maximum canopy uptake capacity during each observation period, notated here as $(\beta+\gamma)_{2000}$. In certain analyses presented in Chapter 3, the maximum PAR intensity used is set at only 1000 μmol photons m^{-2} s^{-1}, e.g., a value for $(\beta+\gamma)_{1000}$ is derived.

The parameters α, β, $(\beta+\gamma)_{2000}$ (e.g., NEE at PAR=2000) and γ were estimated for each site using data from each measurement campaign. Data were pooled for each site and campaign, including measurements in replicate plots during a particular campaign, since fluxes from separate chambers were not of interest and visual examination of the data suggested that the collection of observations (of replicate plots) could be interpreted as a single light response. In botanical garden experiments, each campaign took ca. 1 month, and subsequently included a number of days for each plot.

2.3.2. Aboveground biomass

Sampling in Grillenburg was carried out on a monthly basis during 2004. During each monthly campaign, 10 random quadrats (plots) of 25x25 cm were established in the vicinity of the eddy covariance tower (Appendix) and sampled for biomass and soil properties.

At Mitra in Portugal and in the controlled botanical garden experiments, the green biomass on each plot was measured by clipping the herbaceous mass at stubble height after completion of daily flux measuremens. For all three experimental sites, the

harvested biomass was separated into three growth forms, including grasses, forbs, and legumes, as well as standing dead biomass. From each sample, a sub-sample was selected for LAI determination using an area meter model 3100 (LiCor, Nebraska, USA). The components were oven dried at 90 $^{\circ}$C for 48 hours and weighed to obtain the green and dead biomass dry weight.

2.3.3. Below ground biomass and soil moisture content

After clipping aboveground biomass at the selected plots, soil cores were obtained from the same plots using a hand-driven sampler 8 cm in diameter and 30 cm length (in Grillenburg). Then the soil cores were divided into 5 segments for layers 0-3, 4-7, 8-12, 13-20, 21-30 cm depth at Grillenburg. At other locations, the segments were different as reported below and in Chapter 3. Each layer was then split lengthwise and divided into two approximately equal parts. One set of samples were used to determine pH, soil-water content and soil nutrient properties. The second sets of samples were used for determination of the belowground biomass. All roots from the sub-samples were manually separated, washed and oven dried at 90 °C for 48 hours to determine belowground biomass. After weighing, the root samples were analyzed for nutrient content.

Gravimetric soil moisture for all soil segments was determined by weighing fresh soil samples. The samples were then oven dried at 100 °C until a constant weight was obtained.

At Mitra and in controlled botanical garden experiments, the soil samplers were 3 cm in diameter and 15 cm length; then soil cores were separated into three layers including 0-5, 6-10, 11-15 cm depth (Plate 6) to determine belowground biomass and gravimetric soil moisture content. The soil sampling took place after flux measurements and after clipping the aboveground biomass. pH of the soil samples was determined using a soil-water suspension (1:2.5 vol/vol).

2.3.4. Soil and plant nutrient content

Nitrate and ammonium in the soil were extracted by shaking fresh samples in 1 M KCl (solution to soil ratio 2.5:1, v/v) for 1 hour followed by filtering. The ammonium

concentration was determined by Flow-Injection Analysis (FIA) and nitrate was determined by means of anion-exchange HPLC with UV detection. The leaf and stem portions of grasses, forbes and legumes were analyzed for nitrogen and carbon content. A portion of soil and plant samples were dried and homogenized in a ball mill. The homogenized samples were re-dried in a desiccator to eliminate all the water. A fraction of the dried samples, 4-5 and 15-100 mg of plant and soil samples respectively, were then analyzed to determine their C and N concentrations (%) by means of element analysis. The individual nutrient data of each component were finally pooled as grass and green biomass nutrient content (grass, legume and forb) on a ground area basis.

Plate 6. Illustration of soil cores taken in Mitra. The cores were separated into different layers as described in the text.

Chapter 3
Results

3.1. Temperate grassland at Grillenburg

3.1.1. Microclimate

A climate diagram of Grillenburg is shown in Figure 3.1.1. During the 2004 studies, the growing season started in April and continued until middle of October. No drought was experienced during the entire measurement period and the region has a long record of adequate rainfall throughout the year. During 2004, highest and lowest monthly mean air temperatures were recorded in August (17.5 °C) and January (-2.3 °C), respectively. The highest values of PAR were observed during the vegetative growing season in June and July. Total precipitation in 2004 was 798 mm, which was above the mean annual average of 756 mm recorded in the past 30 years (1971-2000) for the region. The month of July received the highest amount of rainfall (116 mm) on a single day, while the maximum mean monthly record occurred in November (130 mm).

3.1.2.Daily patterns of microclimatic conditions of the study site

Figure 3.1.2. shows the seasonal patterns of microclimatic conditions observed at the study site during the study period and patterns of net ecosystem CO_2 exchange (NEE). NEE, mean daily temperatures and PAR increased steadily from day of year (DOY) 85, attaining a maximum around DOY 210 and eventually declining, and approaching minimum values around DOY 300. Soil moisture values remained high and fluctuations were reflected in the precipitation input pattern.

Fig. 3.1.1. (a) Climate diagram of Grillenburg based on a 30-year period indicating monthly mean air temperature and mean precipitation, (b) mean daily sum of photon flux density (PAR) and mean monthly air temperature during 2004, and (c) mean monthly precipitation during 2004.

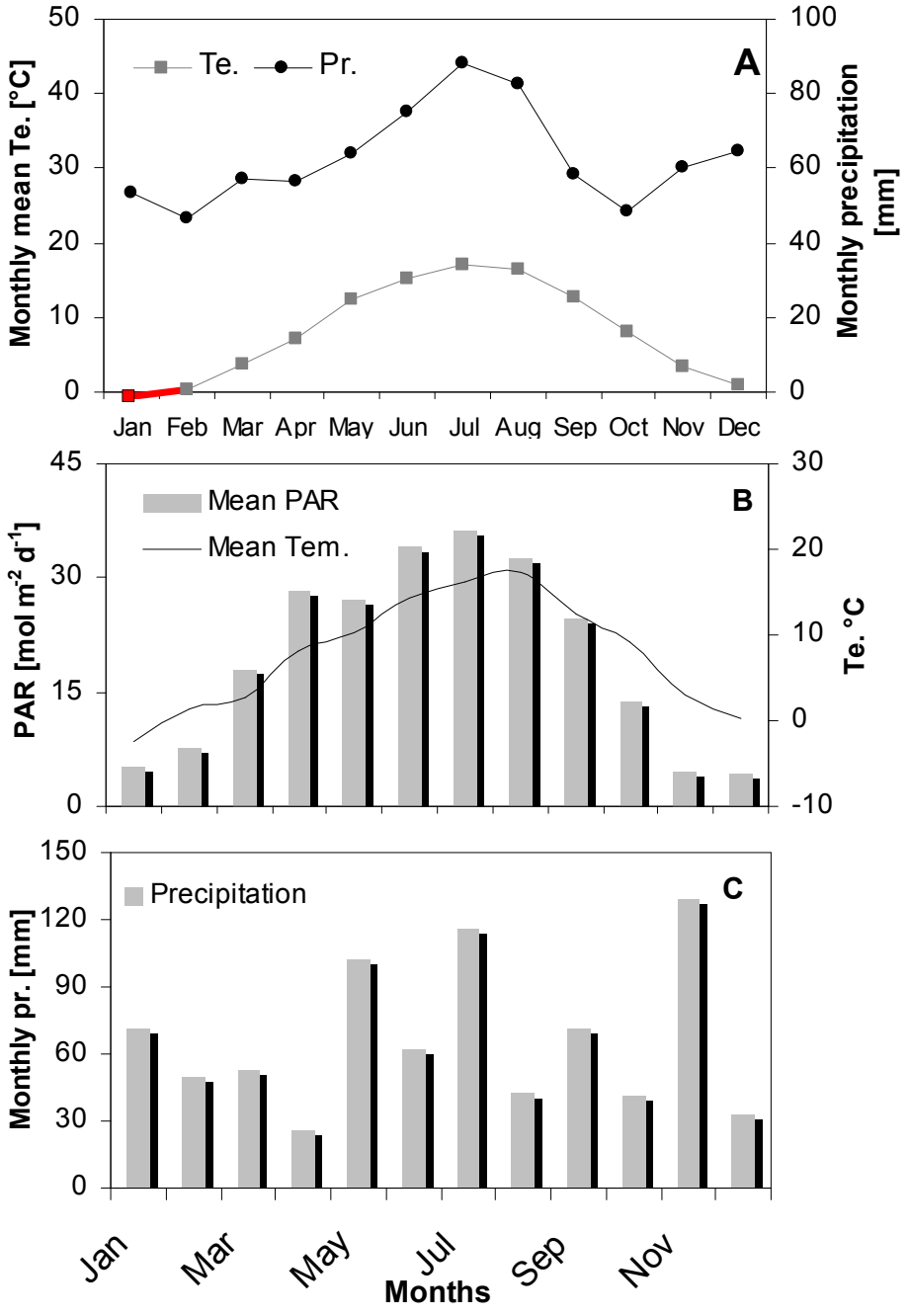
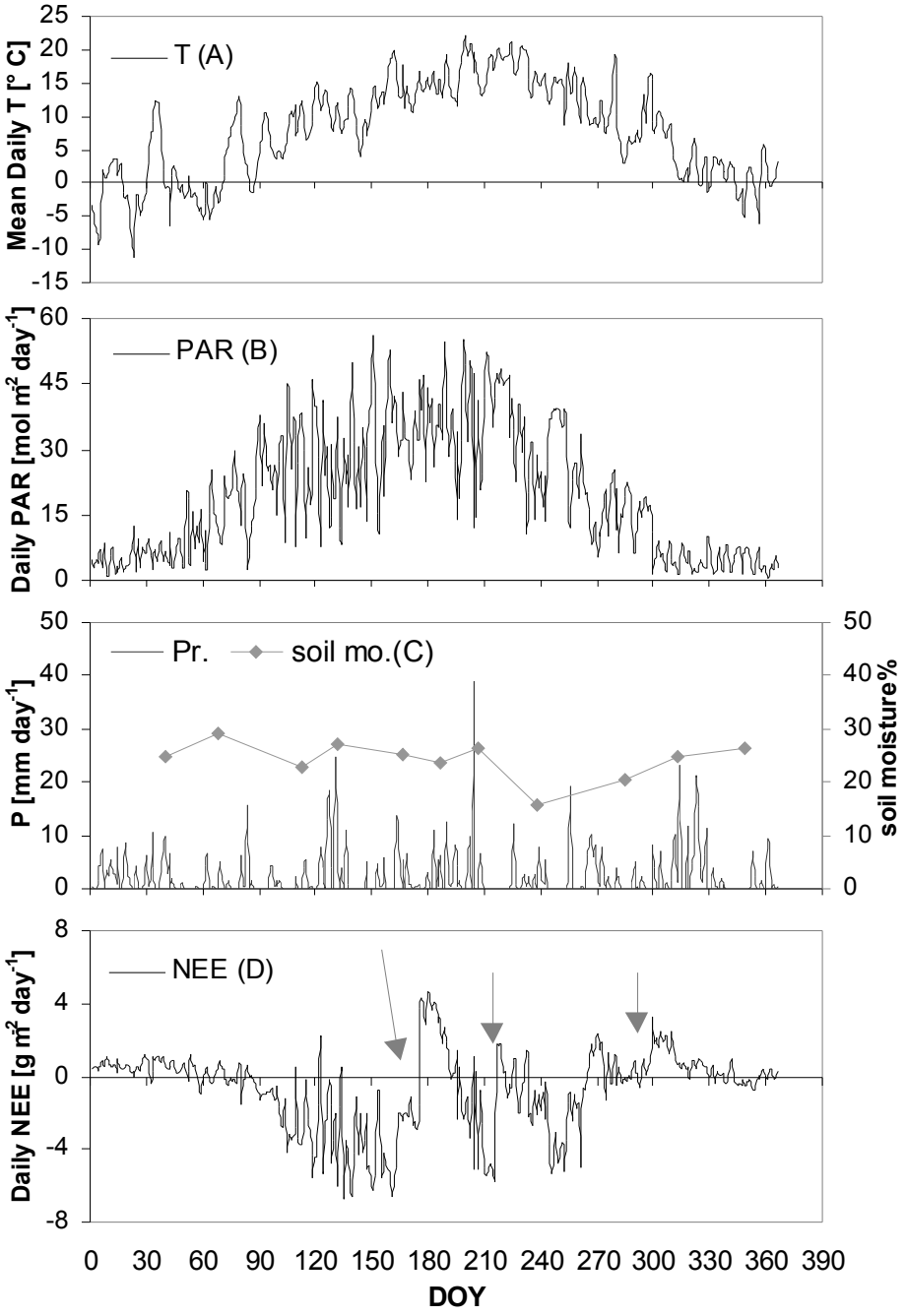


Fig. 3.1.2. The annual course for (a) mean daily air temperature, (b) daily PAR, (c) daily precipitation and soil moisture, and (d) NEE during 2004 in Grillenburg. NEE data are provided by Th. Grünwald (unpublished).



3.1.3. Biomass accumulation, biomass nitrogen content, soil solution N concentrations, and net ecosystem CO_2 exchange in relation to the effects of cutting of aboveground biomass

3.1.3.1. Aboveground and belowground biomass

Aboveground biomass increased slowly after DOY 70, and rapidly after DOY 120 (Figure 3.1.3). As a result of management practices at the study site, which involved mowing, three biomass peaks were recorded but with significantly lower amounts at each subsequent harvest (Figure 3.1.3).

The initial biomass peak of approximately 408 g m^{-2} dry weight was attained around DOY 166. Biomass after cutting was ca. 45 g m^{-2} dry weight. The second biomass peak was recorded around DOY 215 with a mean biomass of about 150 g m^{-2} dry wt. After the second cut, a rapid increase in biomass was recorded until DOY 238, attaining again a dry mass of ca. 150 g d m^{-2}, after which there was significant decline in the biomass until the last cut on DOY 299. Insignificant biomass development was registered thereafter, with virtually no change after DOY 320. Seasonal changes in leaf area index (LAI), were similar to those of live biomass (Figure 3.1.3), with peak values of 5.3, 2.2, 2.0, and 1.2 m^2 m^{-2} on DOY166, 216, 238 and 313, respectively. LAI declined to below 0.45 m^2 m^{-2} at the end of the active growing period.

The seasonal patterns of total live belowground biomass reflected seasonal variations in temperature and rainfall, with the peak root biomass occurring during DOY 180-210 when the temperature was at highest values. Root growth was restricted during the coldest period of the year between late October to end of March (Figure 3.1.4), although a mean value of ca. 800 g m^{-2} was harvested throughout the winter. Two minima in total root biomass of 654 and 631 g m^{-2} were obtained on DOY 113 and 285 respectively, coinciding with beginning and nearly the end of growing season. The maximum observed value was 1200 g m^{-2} on DOY 187 during summer, and coincided phenologically with the end of the foliar stage of development and onset of flowering by the dominant species of the vegetation.

The pattern of changes in above and belowground biomass in both the sites subjected to cutting and those left undisturbed were similar until the first mowing, but differed

thereafter (Figure 3.1.5). Unlike the cut site, aboveground biomass in the uncut site decreased gradually from DOY 166, revealing natural senescence changes. At the end of the growing season, standing biomass in both plots was similar. Belowground biomass at the uncut site reached a peak of 1032 g m^{-2} in early summer (187 DOY), and sharply decreased to 552 g m^{-2} by DOY 285, while at the cut site the decrease in root biomass was more gradual, and also the minimum root biomass was higher (Figure 3.1.5) than at the uncut site (632 g m^{-2} on 285 DOY).

Fig. 3.1.3. Seasonal patterns of biomass and LAI development at Grillenburg during 2004. Days when mowing occurred are shown by arrows.

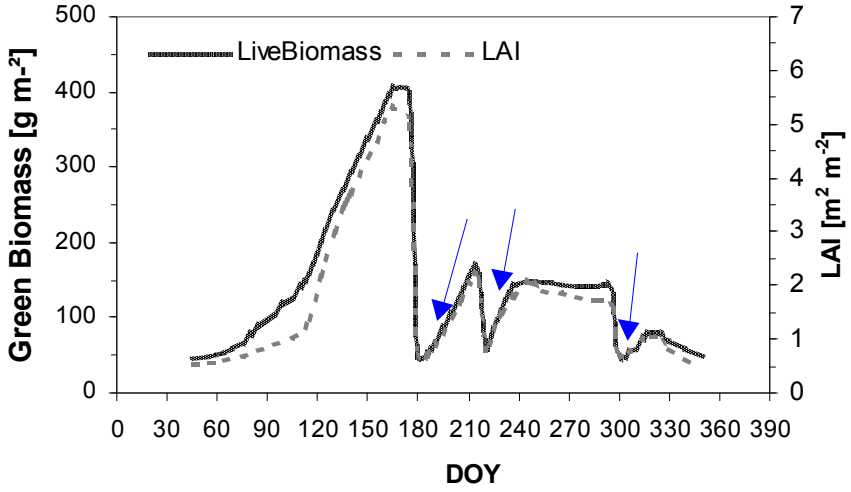


Fig. 3.1.4. Seasonal Changes in above- and belowground biomass during 2004 at the Grillenburg meadow.

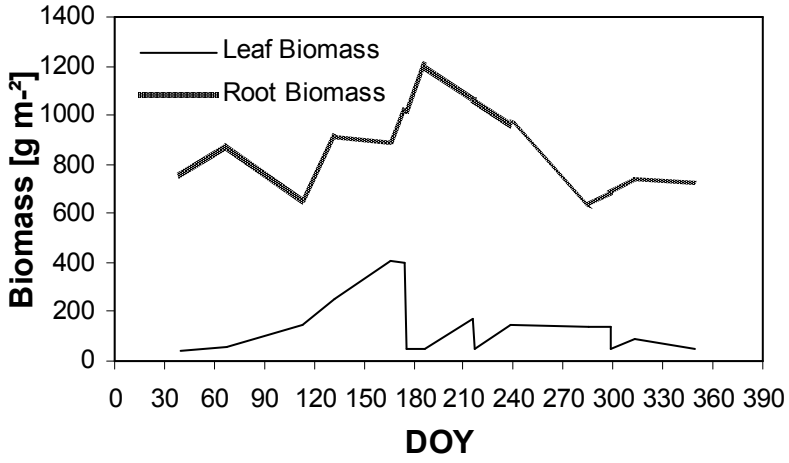
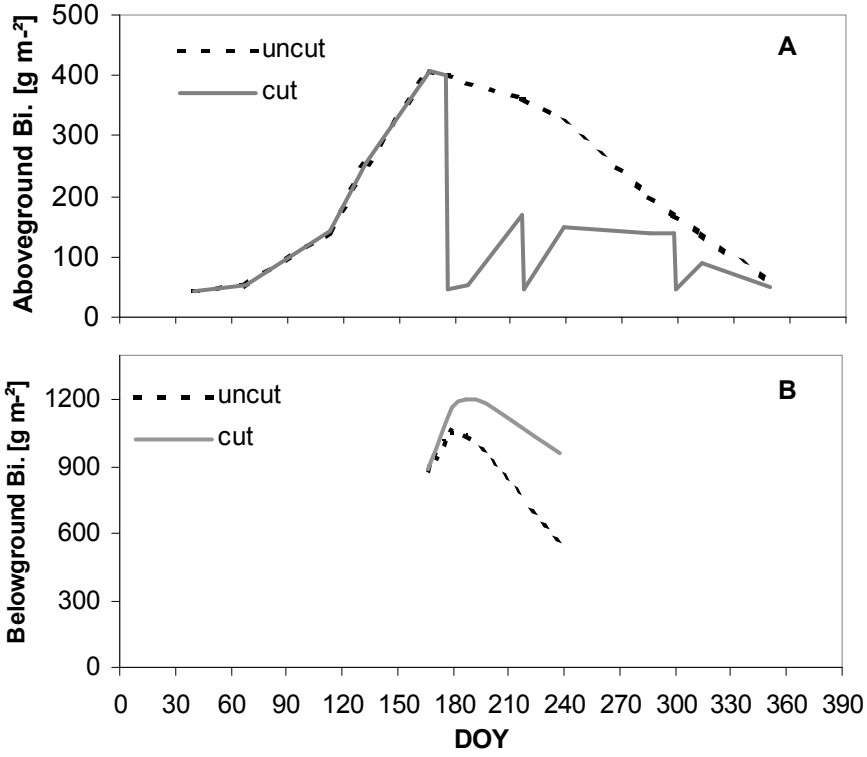


Fig. 3.1.5. (a) Aboveground and (b) belowground biomass in cut and uncut sites during growing season 2004 at Grillenburg



3.1.3.2. Plant nitrogen content

Total nitrogen content in the aboveground total biomass fluctuated according to the pattern of biomass accumulation during the year. Maximum aboveground N (7.68 g m^{-2}) was recorded in early May (Fig. 3.1.6.a), coinciding with peak green biomass. After separating the biomass into different growth forms, which included grasses, forbs and legumes, the grasses accounted for more than 60% of the vegetation, and were therefore the dominant sinks for N. Forbs and legumes played a much lesser role in aboveground N accumulation. Significant decline in aboveground N content occurred after early May, and simultaneously leaf %N concentration increased. This coincided with the first cut and also with the onset of the reproductive phase. A decline in aboveground N was also observed in the uncut plots (Fig. 3.1.8). The decline in foliar N content at the uncut site was, however, much less and occurred obviously along with senescence (discussed further below; Fig. 3.1.8). Leaf %N concentration sharply increased after clipping the meadow (3.43%). Leaf %N concentration was highest on DOY 187 (after cutting aboveground biomass), while lowest concentrations was observed before first harvesting in early-June (Figures 3.1.6.a, b) when the aboveground biomass was mostly at the flowering stage. Leaf C concentration during growing season was stable at 44.5-45.5% but declined to 42.2% after last harvesting on DOY 300 (Fig. 3.1.6.c).

Maximum % root N was observed in early-March (1.52%). N concentration, however, declined thereafter to its lowest value of 1.0% near the end of the growing season on DOY 240, when the root biomass was almost at its highest value (960 g m^{-2}). It later increased and almost resumed peak values as observed on DOY 350. One can assume that the trend continued until March of the following year (before the next growing season). Seasonal changes of root C% exhibited a minimum value on DOY 240 (same as the root N%), which coincided with maximum root biomass accumulation. The maximum value of % root C occurred at the end of growing season, when the root biomass was at its lowest value (631 g m^{-2}, Figure 3.1.7).

Fig. 3.1.6. Seasonal changes in (a) total aboveground leaf N, (b) leaf N concentration and (c) leaf C concentration during the growing season in 2004 at Grillenburg

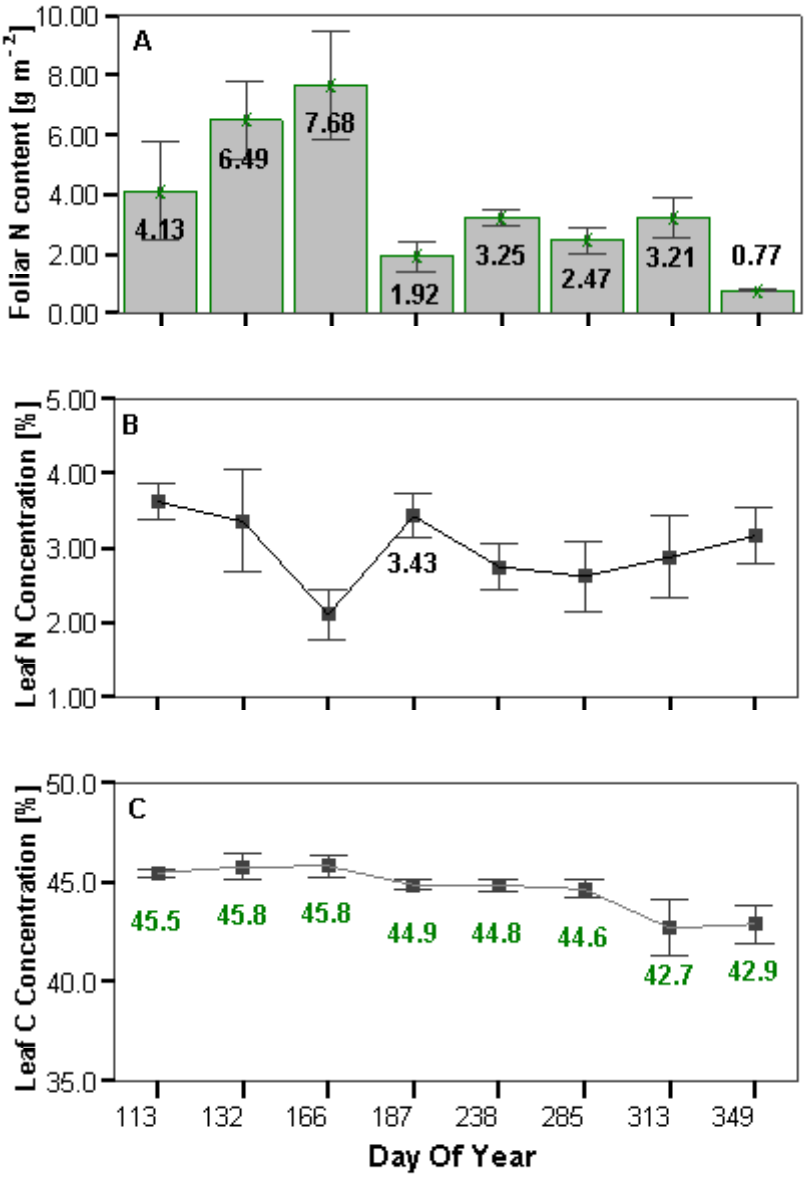


Fig. 3.1.7. Seasonal changes (a) in root biomass, (b) root percent C, and (c) root percent N at the cut site during 2004 in Grillenburg

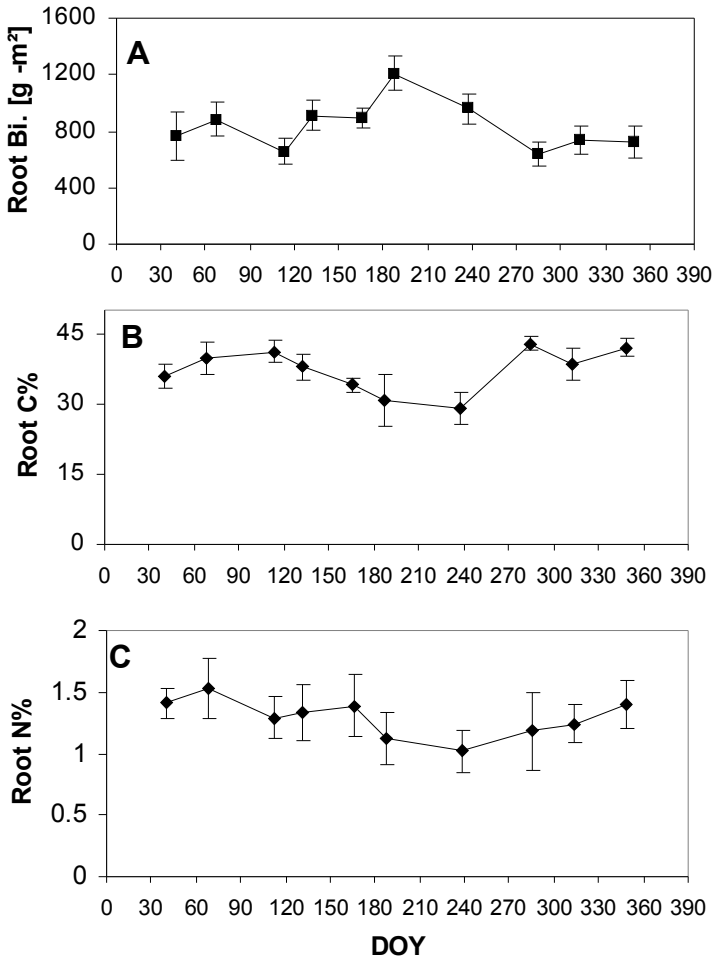
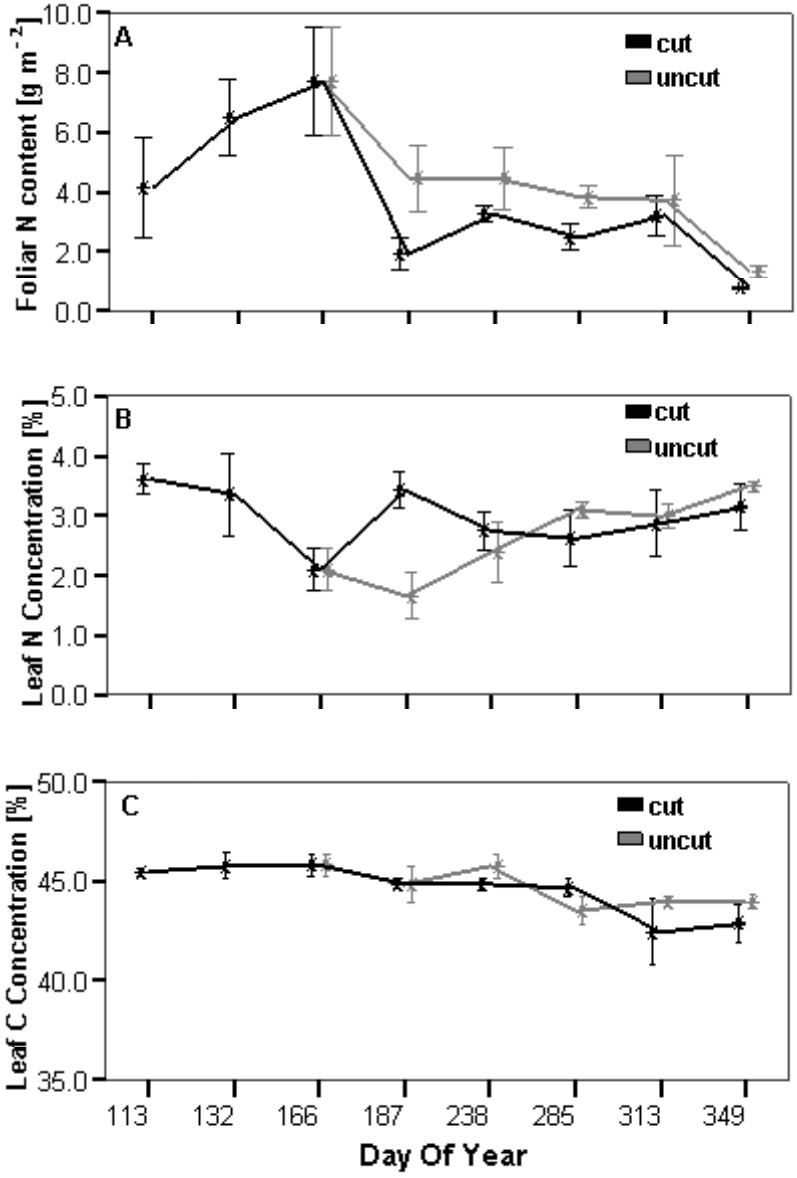


Fig. 3.1.8. (a) Total aboveground foliar N content, (b) percentage leaf N concentration, and (c) leaf C concentrations in cut and uncut sites during the growing season in 2004 at Grillenburg



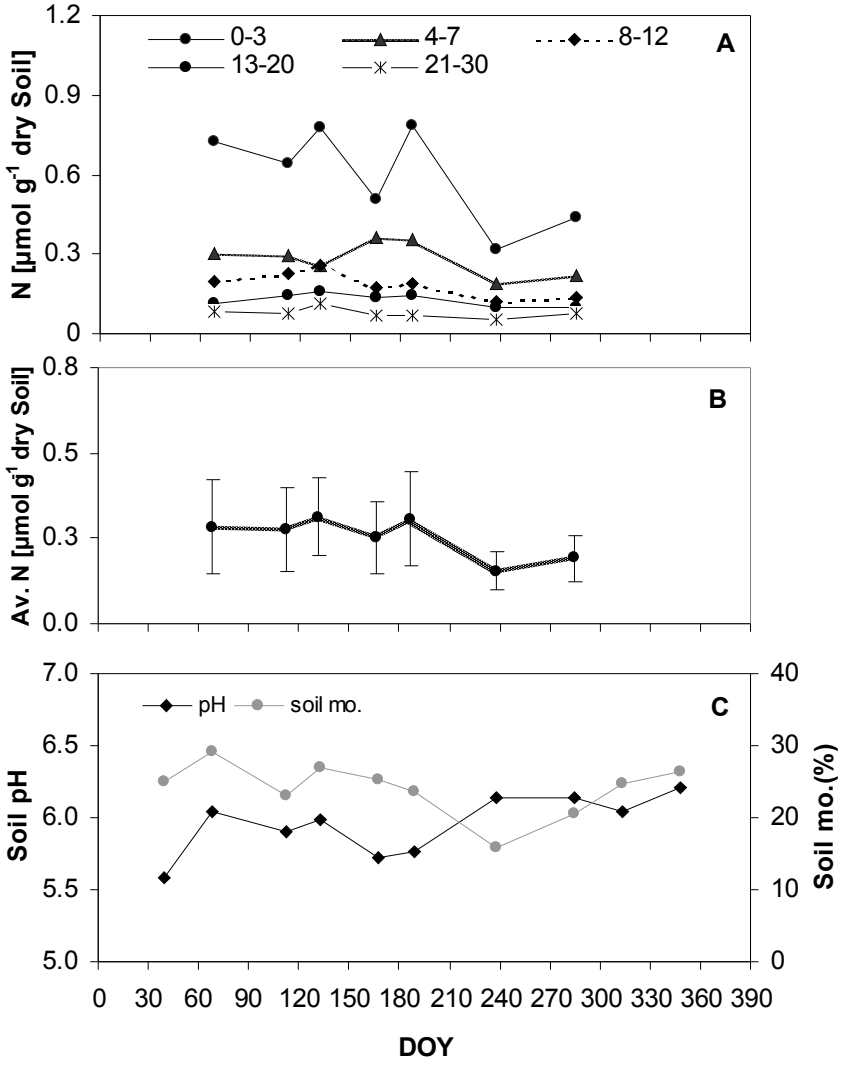
Patterns in total aboveground N and leaf %N content were different at the uncut site (Figures 3.1.8). The maximum aboveground foliar N pool at both sites occurred in early June, and later decreased as cutting or senescence occurred in uncut plots. The decrease in the aboveground N pool was gradual in uncut plots. On the other hand, it was associated with a continuing decrease in leaf %N, while leaf %N in cut plots increased sharply after the first cut. The new foliage is much better supplied with nitrogen, and is probably responsible for decreases in root nitrogen observed at the same time. Percentage leaf C concentration, in the uncut site compared to the cut site was higher and could be attributed to senescing of the leaves in the uncut site compared to the cut site (Figure 3.1.8). Both leaf N and C concentrations in the end of growing season showed similar trends. Differences between the two sites with respect to biomass, LAI, foliar nitrogen and carbon concentration were statistically significant (Table 3.1.2).

3.1.3.3. Changes in soil nutrient and soil moisture content

Available soil N was more concentrated within the top 0-3 cm soil layers and N concentrations decreased with increasing depth (Figure 3.1.9.a). From DOY 113, N concentration in the different soil layers decreased except in mid-June, when there was a significant increase in soil N within the top soil layers (0-7 cm) followed by a significant decline in the 0-3 cm layer. After DOY 200, concentrations of soil N declined again in all the soil layers.

During the study period, highest available N concentration in the soil was recorded in mid-May and early-July (1.56 and 1.51 μmol g^{-1} dry soil), on DOY 132 and 187 respectively, coinciding with a period of rapid root growth (Fig 3.1.7). Thereafter, available N slightly decreased until end of August (DOY 238). Afterwards, soil N remained relatively stable, synchronized with the end of the growing season (Fig 3.1.9.b). The soil water content in the top 27 cm layer (sampled layer) of the soil was approximately 22 to 29 % (g water/g dry soil) in spring season, and declined to 15 % in the late summer. Soil moisture increased again during the snow-free autumn to 26%. Maximum soil pH occurred during summer and autumn when the soil water content was lowest. Average of pH over the whole year was ca. 6 (Figure 3.1.9.c)

Fig. 3.1.9. (a) Concentration of soil N in different layers (b) average of soil N concentration in the soil cores and (c) changes in soil pH and soil water content during 2004



3.1.3.4. Net ecosystem CO_2 exchange

3.1.3.4.1. Eddy covariance measurements

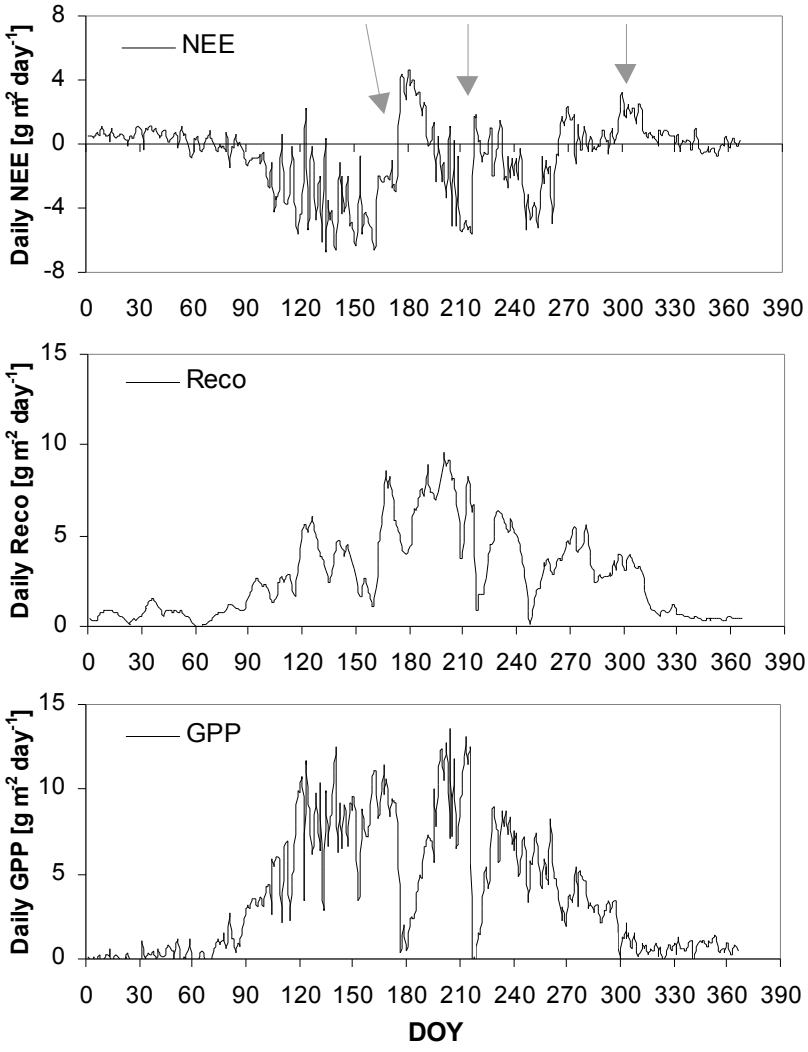
NEE increased significantly between DOY 85 and DOY 165, during which both daily temperature and PAR were on the increase. Lower temperature and PAR as a result of clouds and rains had significant impact on daily NEE values, resulting in lower CO_2 fixation fluxes. Highest and lowest NEE during 2004 were –6.7 (negative NEE represents CO_2 uptake or assimilation by the vegetation) and 4.7 (positive NEE represent ecosystem respiration-R_{eco}) g m^{-2} day^{-1} on DOY 140 and 176, respectively.

Mowing took place on DOY 176, 216 and 299 as indicated by arrows in Figure 3.1.10 and 3.1.11. LAI, biomass, NEE and Reco declined sharply after mowing (Figure 3.1.11). Despite the peak LAI being observed during DOY 160 to 175, highest NEE was recorded between DOY 135 to 160, when the LAI was still below the maximum recorded value (Figures 3.1.11.b, c). Ecosystem respiration (R_{eco}) fluctuated during the vegetative phase and highest R_{eco} were recorded between DOY 160 to 220, differing significantly from the peaks in LAI and NEE (Figure 3.1.11.c).

Rapid vegetation re-growth occurred after every mowing, resulting in subsequent peak LAI values of 2.15 and 2.03 after first and second cuttings, respectively. The respective maximum NEE associated with the peak LAI were –5.7 and –5.2 g m^{-2} d^{-1}. The average of last 10 days of NEE, prior to third cutting was 0.25 (g m^{-2} day $^{-1}$). After the third mowing on DOY 299, re-growth was very slow. This period coincided with the end of the growing season, and was associated with low temperatures and PAR. Large variability in day-to-day NEE were also observed, attributed mostly to varying light levels and temperature. NEE however, decreased slowly but steadily. Thus, before the end of the growing season, NEE reached – 0.5 g m^{-2} d^{-1} on DOY 333, e.g., almost one month after the last cut. After DOY 300, LAI remained almost constant, associated with vegetation senescence, while NEE ranged between -0.6 and 0.5 g C m^{-2} d^{-1} by the end of October (Figures 3.1.11).

During winter and early spring daily rates of net carbon exchange were low, and the difference between NEE and respiration (R_{eco}) was nearly zero. There were appreciable carbon losses, which were greater than carbon uptake especially in early winter, and

Fig. 3.1.10. Daily NEE, R_{eco} and GPP during 2004 in Grillenburg, arrows indicate cutting days. Data from Th. Grünwald (unpublished) and Owen et al. (2007)



this condition continued till early spring (Figure 3.1.12). The cumulative NEE course is shown in Figure 3.1.12. Results show that at the beginning of the year until the end of March, the net ecosystem CO_2 exchange was determined by respiration. Assimilation then gradually increased from early spring (March), reaching its maximum in mid-summer. The time course pattern for GPP was sigmoid, except for the disruptive mowing sessions, during which times the ecosystem reverted into a net CO_2 source before re-growth. The grassland overall was a CO_2 sink with –260 g m^{-2} $year^{-1}$ total CO_2 uptake.

Figure 3.1.11. Seasonal changes in LAI (a), NEE (b), Reco (c), and GPP (c) during 2004. Arrows show harvesting/mowing days. Flux data are from Th. Grünwald (unpublished) and Owen et al. (2007)

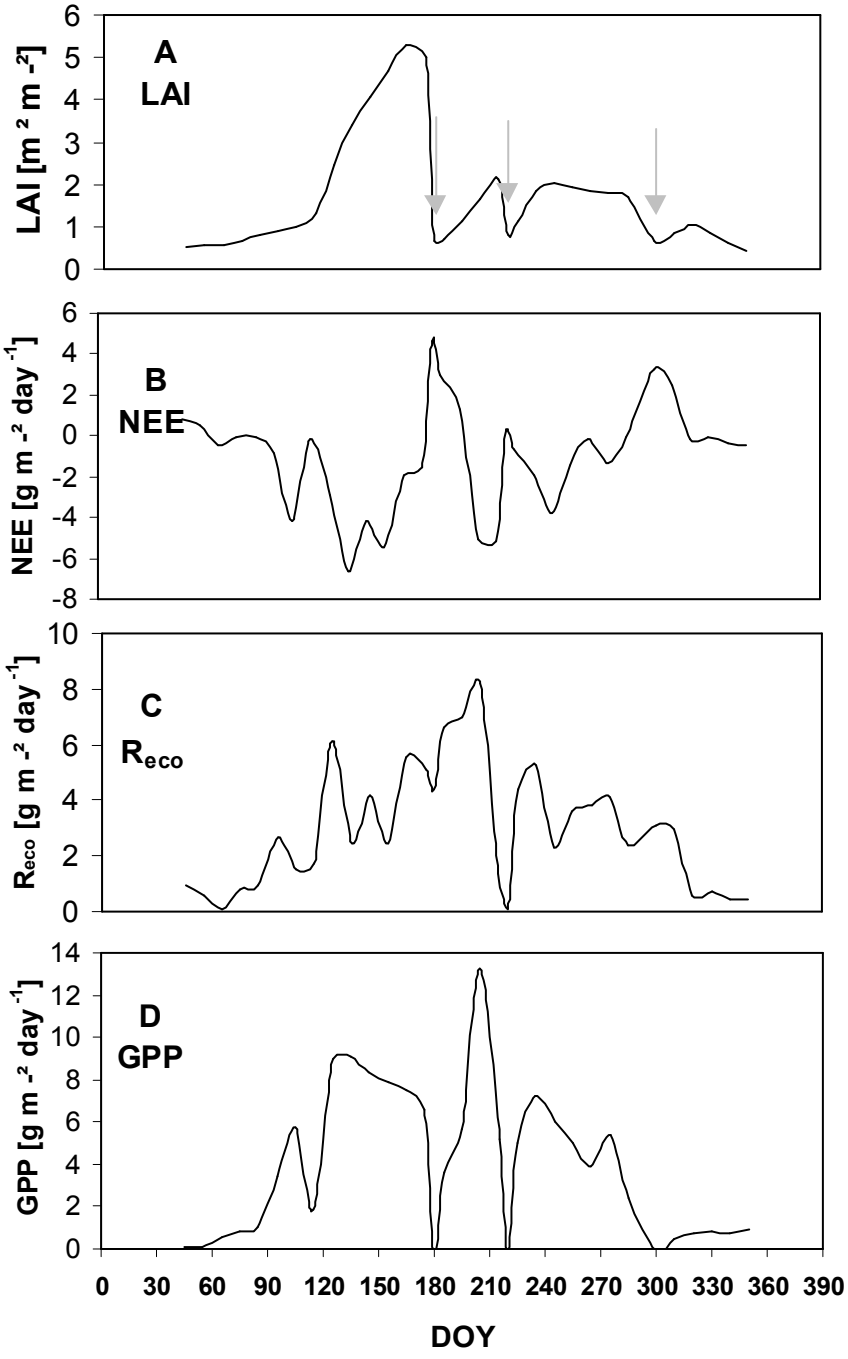
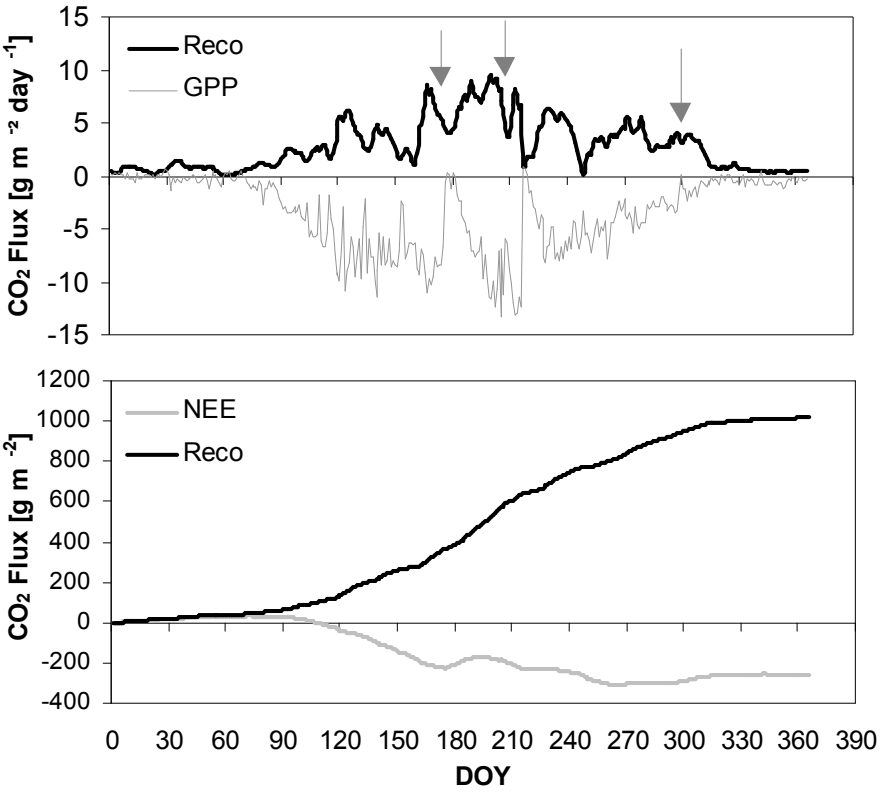


Fig. 3.1.12. Seasonal patterns of daily GPP and R_{eco} (above) and cumulative NEE and R_{eco} (below) during 2004 at Grillenburg. Flux data are from Th. Grünwald (unpublished) and Owen et al. (2007)



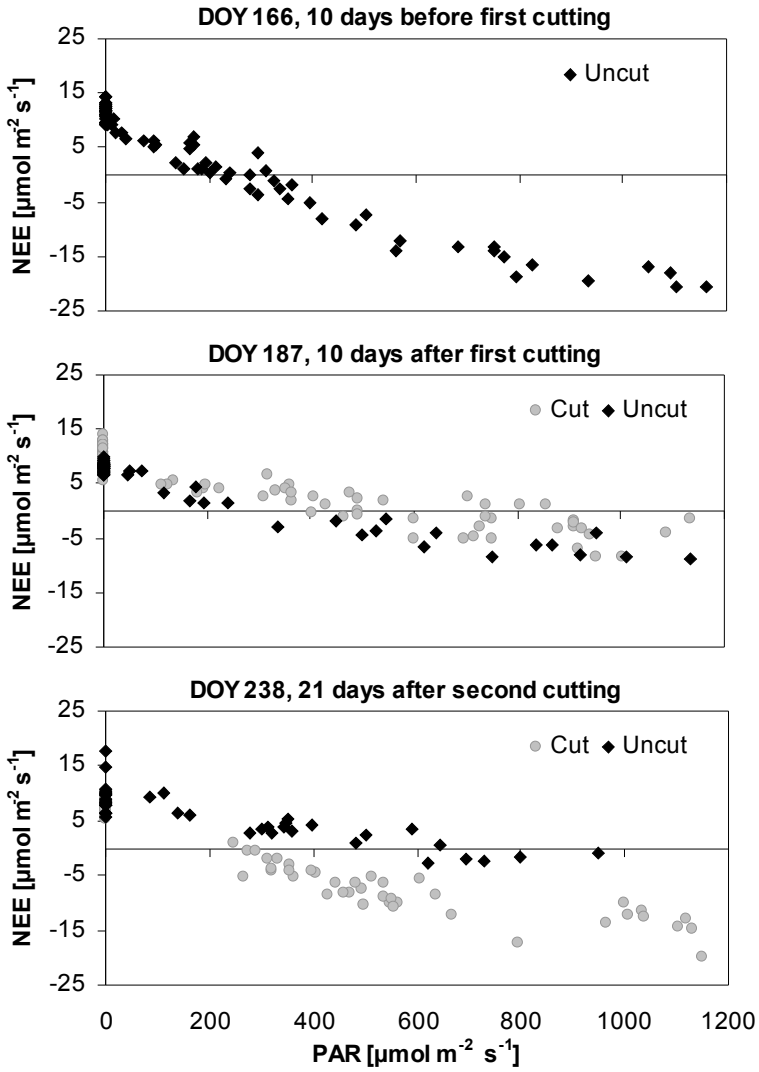
3.1.3.4.2. Net ecosystem exchange measurements with chambers

Chamber measurements allow us to relate CO_2 flux rates directly to the ecosystem structure being observed. They allow one to examine direct effects of cutting on NEE, which is not possible from the eddy covariance studies discussed above. Daily course of net ecosystem exchange (NEE) at two sites, consisting of cut and uncut plots, were observed in three campaigns using both light and dark chambers. Plotting the observations versus PAR, as shown in Figure 3.2.13, one can see that there is a significant influence of cutting on Nee. A negative value of NEE indicates a net flux of CO_2 from the atmosphere to the ecosystem, i.e., a gain in carbon by the ecosystem. Also shown are the predicted values after fitting the hyperbolic light response model to the data.

Apparent from the data are that the response at both locations was the same on DOY 166 (discussed further below in terms of parameter determinations – Fig. 3.2.14). Ten days after the first cut, the response of both meadow stands appears to be rather similar, but the structure is extremely different as described above. Closer inspection indicates some differences. Under certain conditions, the ecosystem respiration seems to be higher at the cut site (scatter at PAR = 0). But the high N content of young growing leaves results in uptake of CO_2 at high PAR. In the case of the uncut stand, senescence appears to have reduced the uptake capacity of the vegetation. After the second cut, the cut vegetation again recovers and exhibits relatively high CO_2 uptake at high PAR, enough to overcome respiration and result in quite negative NEE. In the uncut vegetation, continued senescence leads to even lower uptake of CO_2, which is near compensation at high values of PAR.

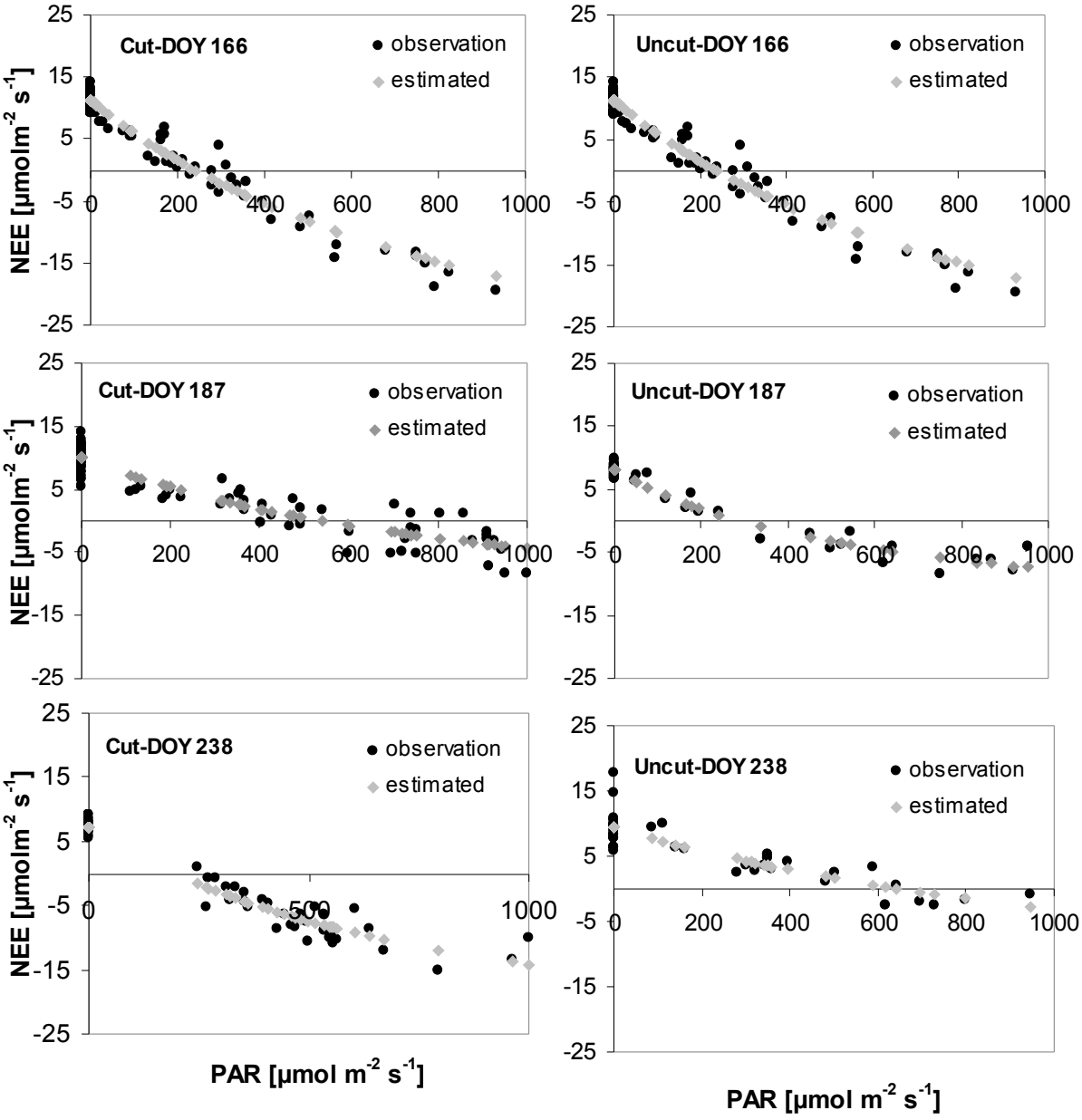
In order to harmonise results and obtain a clearer picture of these changes, data from the different measurement periods were analyzed with the simple hyperbolic light response model (see Materials and Methods), which takes into account the differences in PAR during respective measurements. The relative similarity between estimated and observed flux data considering all campaigns at different sites, e.g. R^2 value of the model fit, ranged between 0.85 and 0.95. Thus, a good description of the observed data is obtained in each and every case.

Fig. 3.1.13. Comparison of NEE in two cut and uncut sites during three campaigns in 2004 at Grillenburg. Cuts were made on DOY 176 and on 216. Thus, data represent response 10 days before the first cut, 11 days after the first cut, and 22 days after the second cut. Number of plots = 3.



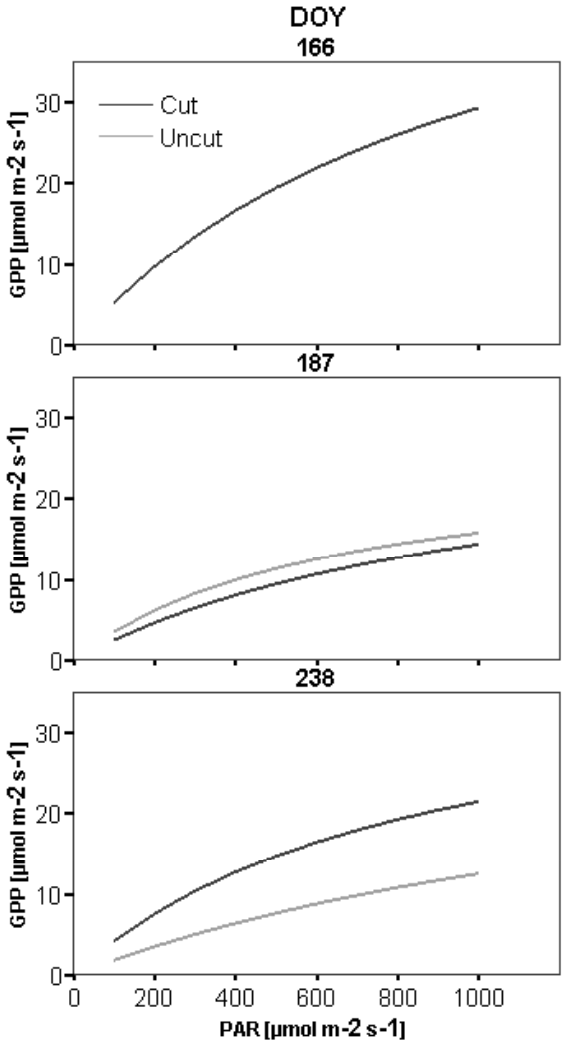
Values for the parameters α, β, β_{2000}, and γ for all measurement days derived from the model, are shown in Table 3.2.1. Furthermore, the relationship between estimated and observed NEE is shown in Figure 3.1.14. The model allows us to separate net ecosystem exchange (NEE) into its major components, namely gross primary production (GPP) and

Fig. 3.1.14.Measured and estimated NEE during three campaigns examining the cut and uncut sites in the study plots at Grillenburg in 2004



ecosystem respiration (Reco). Adjusting for differences in ecosystem respiration, the relationship between GPP and different PAR intensity at the two sites was constructed from model-based data (Fig. 3.1.15). After cutting (DOY 187), the GPP response curve obtained at the uncut site was above that at the cut site, but the difference was small, indicating that natural senescence phenomena and aging of the stand can play an

Fig. 3.1.15. Comparison of GPP-light response curves in both cut and uncut sites for three campaigns during 2004 in Grillenburg.



extremely important role in carbon exchange. However, during the next campaign (DOY 238) carried out 22 days after the second cutting, GPP at the cut site was higher than in the uncut site due to vegetation recovery. GPP at the uncut site continued to decrease along with senescence and decreases in leaf %N. Different patterns of respiration, aboveground biomass and LAI were observed in the cut and uncut sites during the three campaigns (Fig. 3.1.16) The results show higher respiration (γ) in the cut site on DOY 178, 10 days after first cutting, than in the uncut site (Fig. 3.1.16).

Fig. 3.1.16. Biomass and respiration at the cut and uncut sites during 2004 at Grillenburg

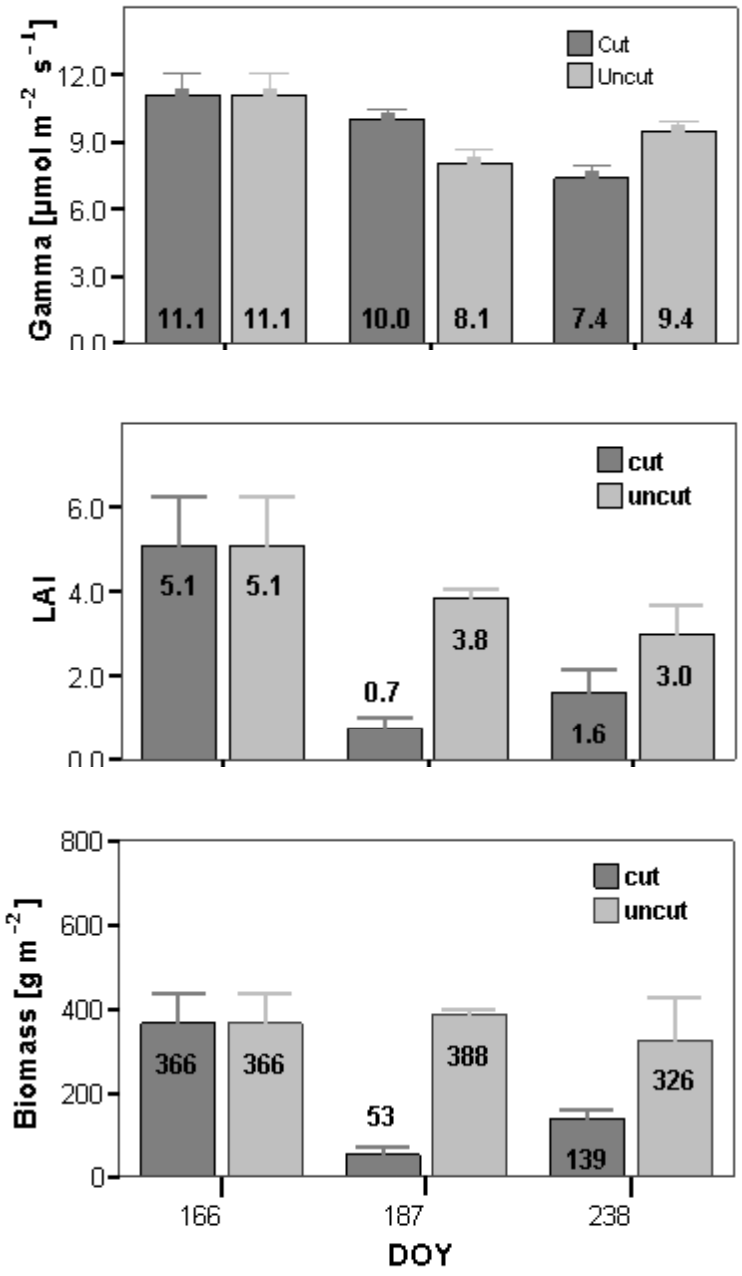


Table 3.1.1. Model parameters for NEE from the analysis shown in Fig. 3.1.14

Data	Alpha	Beta	Gamma	R^2	Site*	Campaign
83	0.06	59.09	11.25	0.97	uncut	1
60	0.04	25.76	8.10	0.97	uncut	2
41	0.02	34.52	9.33	0.75	uncut	3
83	0.06	59.09	11.25	0.97	cut	1
127	0.03	30.04	9.96	0.90	cut	2
78	0.05	39.71	7.32	0.96	cut	3

* Average of three plots

Table 3.1.2. Comparison of aboveground biomass, LAI, and nutrient properties in cut and uncut sites during 2004 in Grillenburg.

Dependent Variable: Biomass [g m-2]

Source	Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	1011701.3	9	112411.3	49.3	.000
Intercept	1736401.9	1	1736401.9	761.3	.000
SITE	153554.1	1	153554.1	67.3	.000
CAMPAIGN	613412.9	4	153353.2	67.2	.000
SITE* CAMPAIGN	178387.4	4	44596.8	19.6	**.000**
Error	100360.3	44	2280.9		
Total	2768472.6	54			
Corrected Total	1112061.6	53			

Dependent Variable: LAI

Source	Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	171.9	9	19.1	30.3	.000
Intercept	249.5	1	249.5	396.0	.000
SITE	12.9	1	12.9	20.5	.000
CAMPAIGN	126.3	4	31.6	50.1	.000
SITE* CAMPAIGN	15.0	4	3.7	5.9	**.001**
Error	27.7	44	.6		
Total	458.4	54			
Corrected Total	199.6	53			

Table 3.1.2. Continued

Dependent Variable: Foliar N content [g m-2]

Source	Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	286.6	13	22.0	16.9	.000
Intercept	748.5	1	748.5	573.4	.000
SITE	11.2	1	11.2	8.6	.005
CAMPAIGN	252.3	7	36.0	27.6	.000
SITE * CAMPAIGN	8.7	5	1.7	1.3	**.270**
Error	58.7	45	1.3		
Total	1393.5	59			
Corrected Total	345.3	58			

Dependent Variable: Leaf N Concentration [%]

Source	Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	17.9	13	1.4	8.1	.000
Intercept	359.7	1	359.7	2125.5	.000
SITE	.4	1	.4	2.5	.123
CAMPAIGN	9.8	7	1.4	8.3	.000
SITE * CAMPAIGN	6.3	5	1.3	7.4	**.000**
Error	7.6	45	.2		
Total	478.9	59			
Corrected Total	25.5	58			

Dependent Variable: Leaf C Concentration [%]

Source	Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	56.6	13	4.4	10.9	.000
Intercept	88449.1	1	88449.1	221561.8	.000
SITE	1.3	1	1.3	3.2	.078
CAMPAIGN	50.5	7	7.2	18.1	**.000**
SITE * CAMPAIGN	6.8	5	1.4	3.4	.011
Error	18.0	45	.4		
Total	118523.0	59			
Corrected Total	74.6	58			

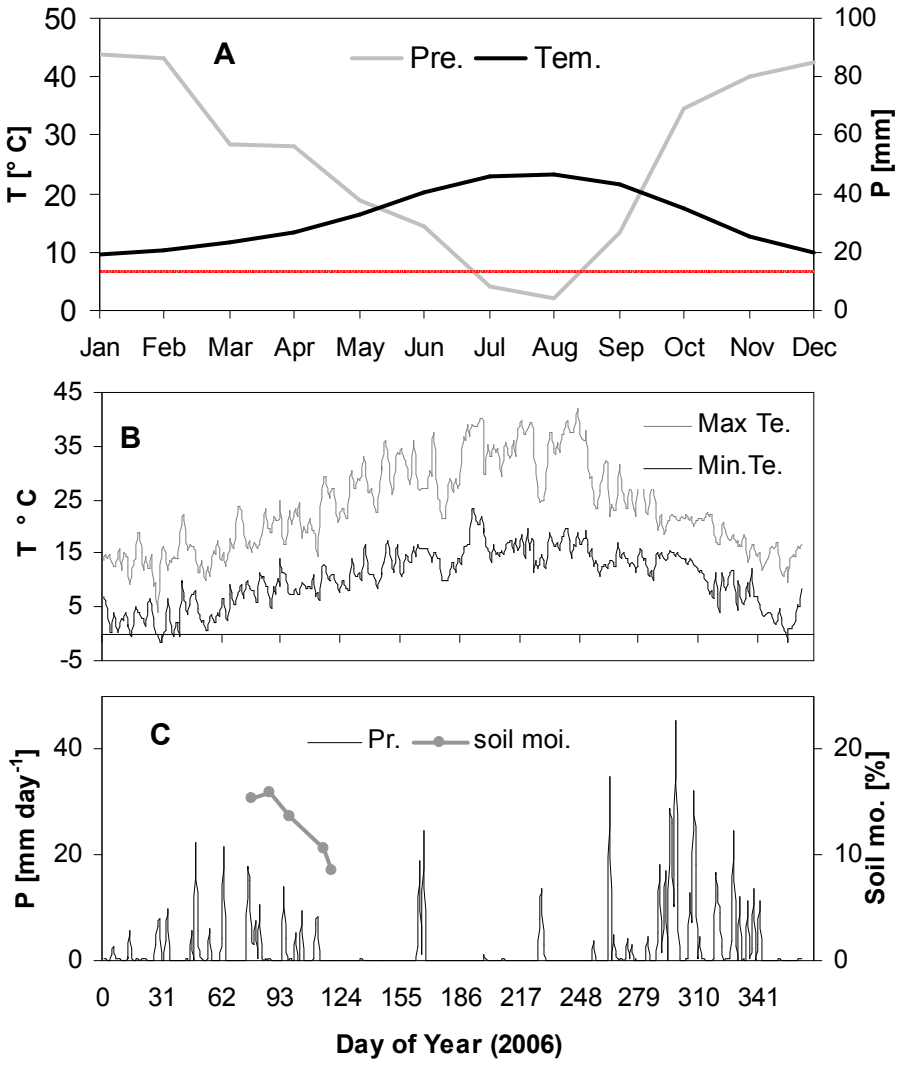
3.2. Mediterranean grassland at Herdade da Mitra, Portugal

3.2.1. Climate and weather parameters during study period

Figure 3.2.1 shows a climate diagram of the study site at Herdade da Mitra (Evora, Portugal) constructed from data accumulated over a 30-year period (1960-1990). The region is influenced by a Mediterranean type of climate with dry periods being experienced from mid-May till mid-September. Wet seasons start from the month of October and extend into middle of April, with some seasonal variations from year to year. Nevertheless, the general patterns are usually predictable. Maximum and minimum mean monthly temperatures occur in August (23.5 °C) and January (9 °C) respectively. Most of the annual precipitation (630 mm) is received during autumn and winter. More than 80% of annual precipitation occurs between October and April.

During the measurement period (early-March to late-May in 2006), weather variables were continuously monitored at an eddy covariance tower established 100 m away from the experimental site. Daily maximum air temperatures increased rapidly with increasing radiation input from 11.6 °C in early March to 31.1 °C at the end of the measurement period in late-May (Figure. 3.2.1.c). Minimum diurnal temperatures were initially low (1.3 °C) and frost occurred in the area on one occasion during early March. Mean minimum diurnal temperatures however, increased steadily and reached 16.8 °C in May. Low temperature limitation occurs during mid-December to the end of January and vegetation growth stops during this period. The peak production of grassland vegetation occurs in April and May (Figure 3.2.1). Soil moisture during the measurement period until DOY 101 was almost constant (ca. 15%) but later (DOY 122), due to reduction in precipitation, soil moisture declined to 8.5% (Figure 3.2.2).

Fig. 3.2.1. (a) Climate diagram of Herdade da Mitra constructed using a 30-year period, (b) daily mean maximal and minimal temperature, and (c) daily precipitation and soil moisture during the study period in 2006.

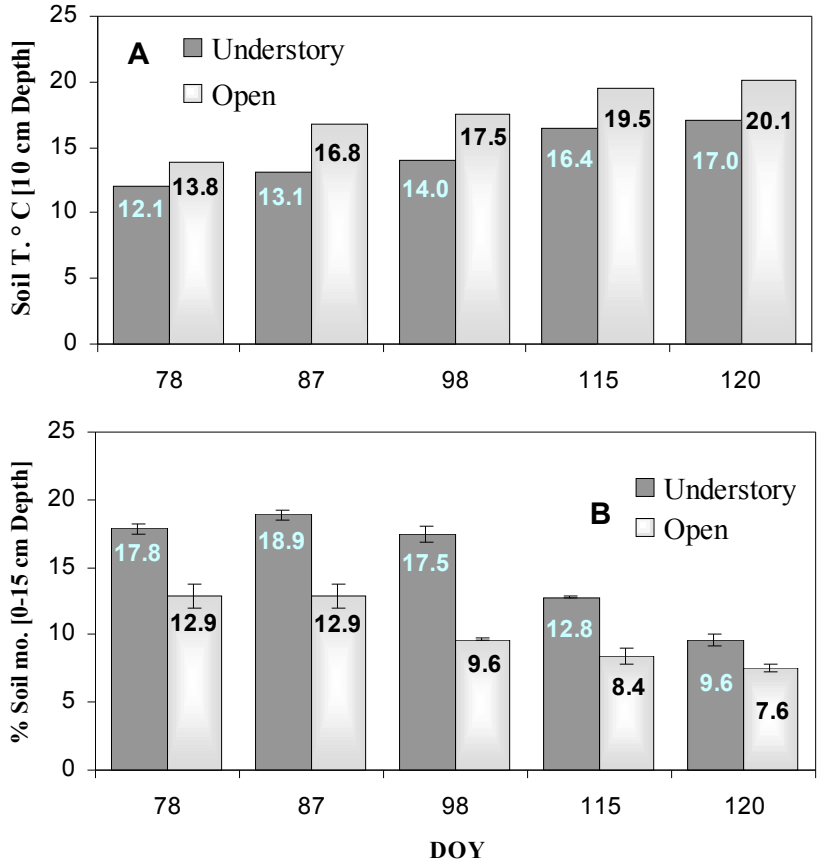


3.2.2.Effect of tree canopies on herbaceous vegetation, its microclimate, and on montado ecosystem heterogeneity

3.2.2.1.Tree canopy effects and microclimate

Understory locations in the montado below trees, compared to open locations receive less light, consequently soil temperature as an important factor influencing ecosystem respiration is lower. Fig.3.2.2.a shows mean soil temperature between 1 and 2 PM in early afternoon at 10 cm depth during the study period in these two locations. There was significant difference between the locations using paired-samples t-test ($p<0.001$). Figure 3.2.2.b shows the significant differences between the the locations ($p<0.005$) in soil moisture, which declines strongly at the end of growing season in May.

Fig. 3.2.2. (a) Comparison of soil temperature at 10 cm depth and (b) mean soil moisture (0-15 cm) at understory and open locations at midday during the study period in 2006. Number of plots in each sample was three. Bars indicate standard deviation.



3.2.2.2. Tree canopy influences on seasonal patterns in biomass development and plant and soil nitrogen stocks in the herbaceous vegetation

Significant variations in structure were obvious at the different locations studied, so data were grouped according to the two distinct locations, open and shade/understory below the trees. Larger biomass accumulation occurred in the open locations outside the tree canopies as compared to understory (Fig. 3.2.3.a). Similar results were observed for belowground biomass, with the open locations initially having higher root mass than the understory (92 and 73 g m-² respectively). Maximum aboveground biomass in both sites occurred on ca. DOY 114. Foliar N and C concentration in the understory and open sites showed similar patterns, with decreasing amounts during the growing season. There was no significant difference between percentage foliar N at the open site compared to that in tree understory (Table 3.2.1).

Fig. 3.2.3. Seasonal changes in green above- and below ground biomass in open and understory sites during the growing season in 2006. Number of plots in each sample was three. Bars indicate standard deviation.

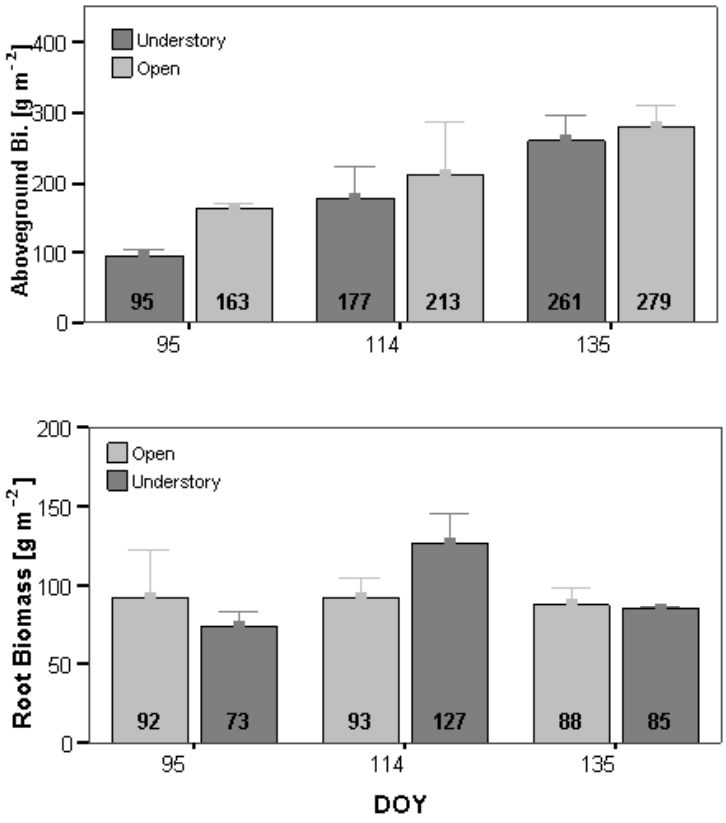
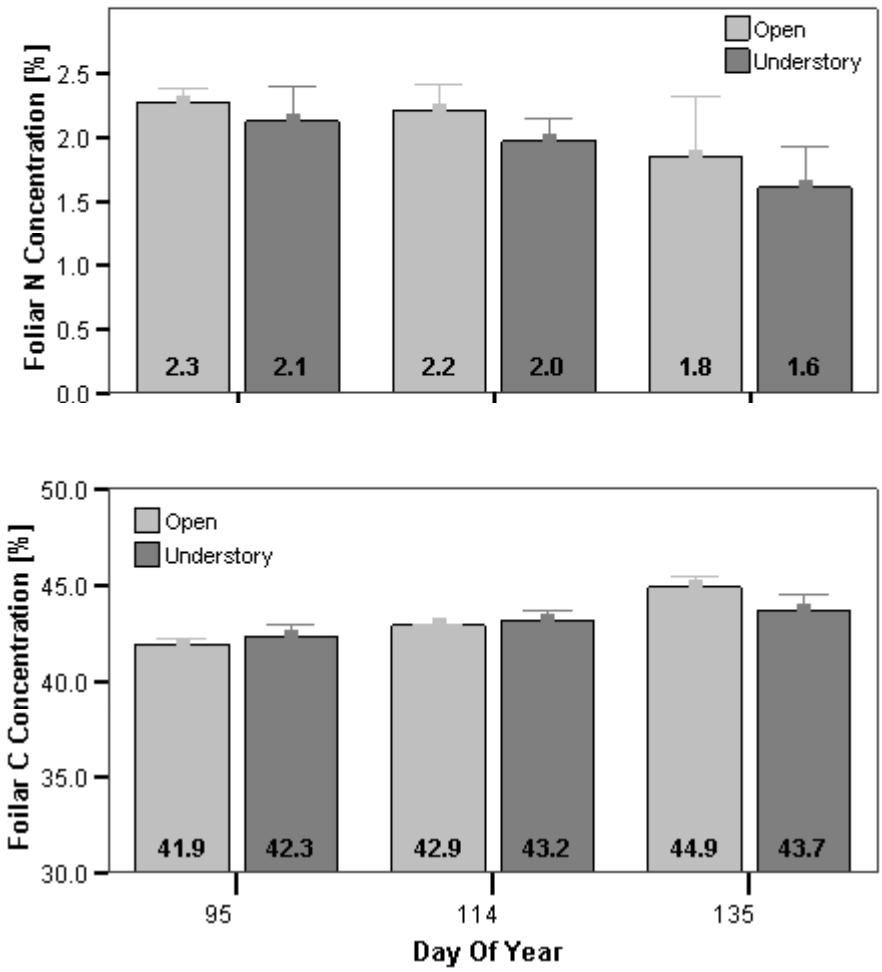


Fig. 3.2.4. Foliar nitrogen concentration in open and understory sites during growing season in 2006. Number of plots in each sample was three. Bars indicate standard deviation.



Foliar C concentration at both sites were similar and increased with senescing of the vegetation, e.g. in the open site on DOY 95 C% was 41.9% while on DOY 135 it increased to 44.9%.

Root N concentration in both sites remained relatively constant throughout the growing period, with insignificant increases from 0.9% at the beginning to 1.11% at the end of the growing season (Figure 3.2.5). In contrast root C concentration showed gradual increase during the growing season from 26.2% to 36.5% at the end of the season. Significant

difference occurred between % root C values in open (26%) and understory (32.5%) locations, with the understorey showing higher C concentrations ($p<0.07$), but not significant differences in root N concentration (Figure 3.2.5)

Soil nitrogen content also varied significantly between the two locations, especially within the 0-7 cm soil layer (total soil N concentration of 0.08% and 0.17% in the open and understory sites, respectively). Differences were also observed between the layers. Soil C concentrations were similar to soil N concentration, with higher C concentration in the shallow soil layers, as well as in the understory. Soil C concentration in the first 0-3 cm layers were 0.08% and 2.3% in the open and understory respectively, while the respective concentrations in the second layer (8-12 cm) were 0.6% and 0.7% (Fig.3.2.6).

Fig. 3.2.5. Changes in root % N and C concentrations in open and understory locations during three campaigns. Number of plots in each sample was three. Bars indicate standard deviation.

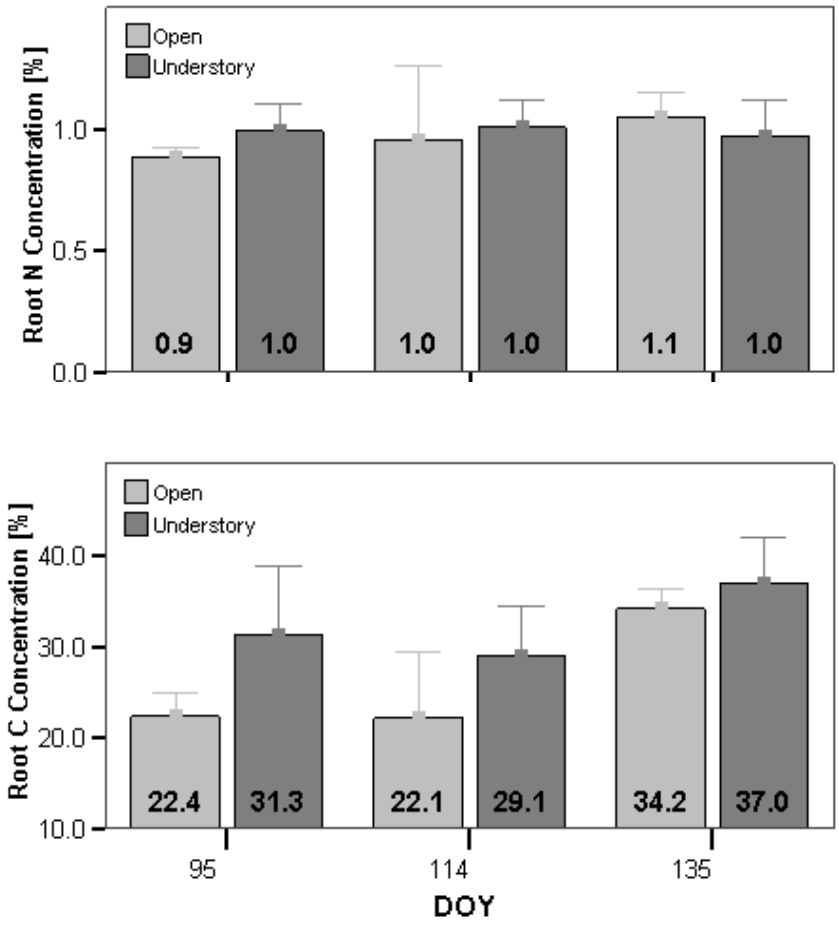


Figure 3.2.6. Soil characteristics in the open and understory locations within two soil layers (0-7 cm and 8-12 cm) on DOY 135. Number of plots in each sample was three. Bars indicate standard deviation.

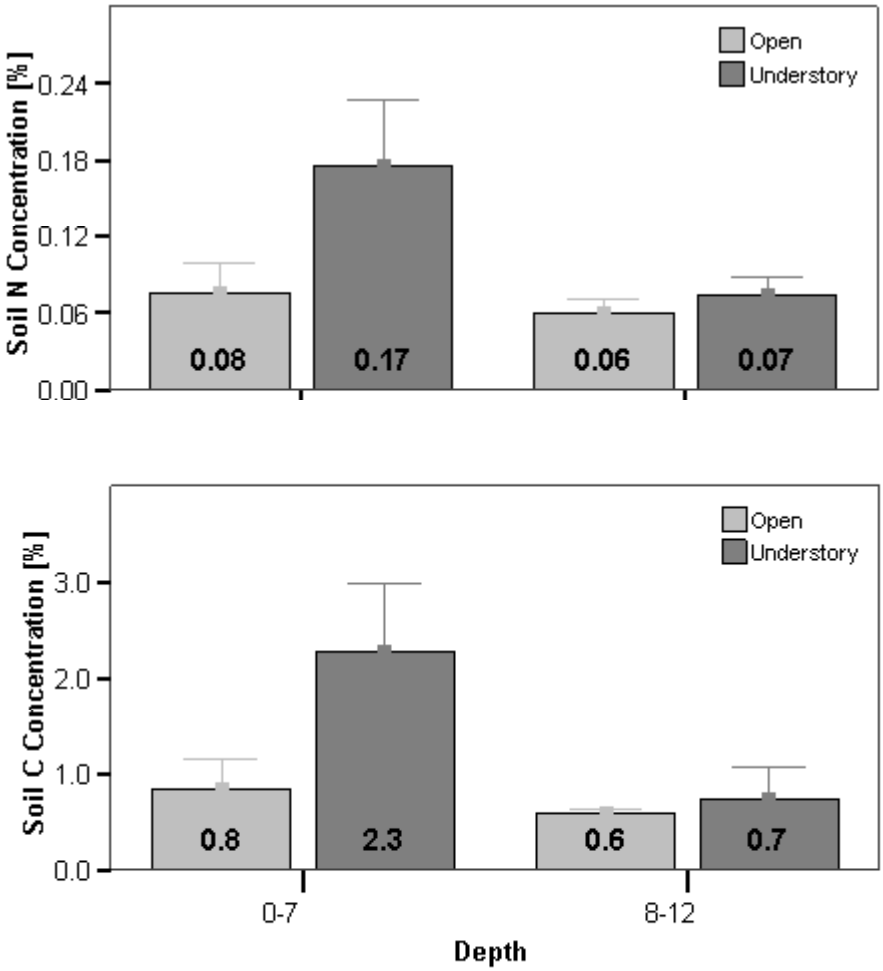


Table 3.2.1. shows statistical analysis of differences between soil, above- and belowground biomass and nutrient properties in the understory and open sites. There was significant difference between root C concentration ($p<0.07$). The first layer of soil (0-7 cm) showed significant difference between C and N soil concentration within two sites ($p<0.01$), but not significant differences between the second layers (8-12 cm).

Table 3.2.1. Statistical analysis of above- and belowground biomass, soil characteristics and nutrient distribution in open and understory locations.

Open and Understory

Variables	Sum of Squares	df	Mean Square	F	Sig.
Aboveground Bi. [g m-2]	11857.435	1	11857.435	1.73	.201
Foliar N Concentration [%]	.146	1	.146	1.29	.269
Foilar C Concentration [%]	.963	1	.963	.847	.367

Variables	Sum of Squares	df	Mean Square	F	Sig.
Root N Concentration [%]	.003	1	.003	.13	.72
Root C Concentration [%]	174.349	1	174.349	3.80	.07
Root Biomass [g m-2]	5822.609	1	5822.609	2.49	.13

Variables	Sum of Squares	df	Mean Square	F	Sig.
Soil N Concentration [%] 0-7	.020	1	.020	9.58	.02
Soil C Concentration [%] 0-7	4.101	1	4.101	11	.01
Soil N Concentration [%] Total	.006	1	.006	11	.01
Soil C Concentration [%] Total	1.247	1	1.247	11	.01
Soil N Concentration [%] 8-12	.000	1	.000	1.77	.23
Soil C Concentration [%] 8-12	.043	1	.043	.52	.49

3.2.2.3. Tree canopy influences on diurnal and seasonal patterns in net ecosystem CO_2 exchange

The daily course of net ecosystem exchange in two location, understory and open, was measured during 3 campaigns (DOY 80, 90 and 102) in order to monitor diurnal and seasonal patterns of CO_2 exchange. The results are shown in Figure 3.2.7.a where all observations are plotted against PAR, considering radiation alone to explain the diurnal variation. Parameter values for the hyperbolic light response model and goodness of fit for each campaign and location are given in Table 3.2.2. The values of R^2 are quite high indicating again that the model provides a good explanation of the data. Simulated response curves for GPP are shown in Figure 3.2.8. These are obtained by varying PAR and adding Reco (gamma) to estimated values of NEE. The maximum PAR used was 1000 μmol m^{-2} s^{-2}, referred to in the comparisons below as GPP-1000.

Fig. 3.2.7. (a) Comparison of NEE data obtained from chamber measurement and (b) potential GPP light response curves using a rectangular hyperbolic model, as observed during 3 campaigns on DOY 80, 90 and 102.

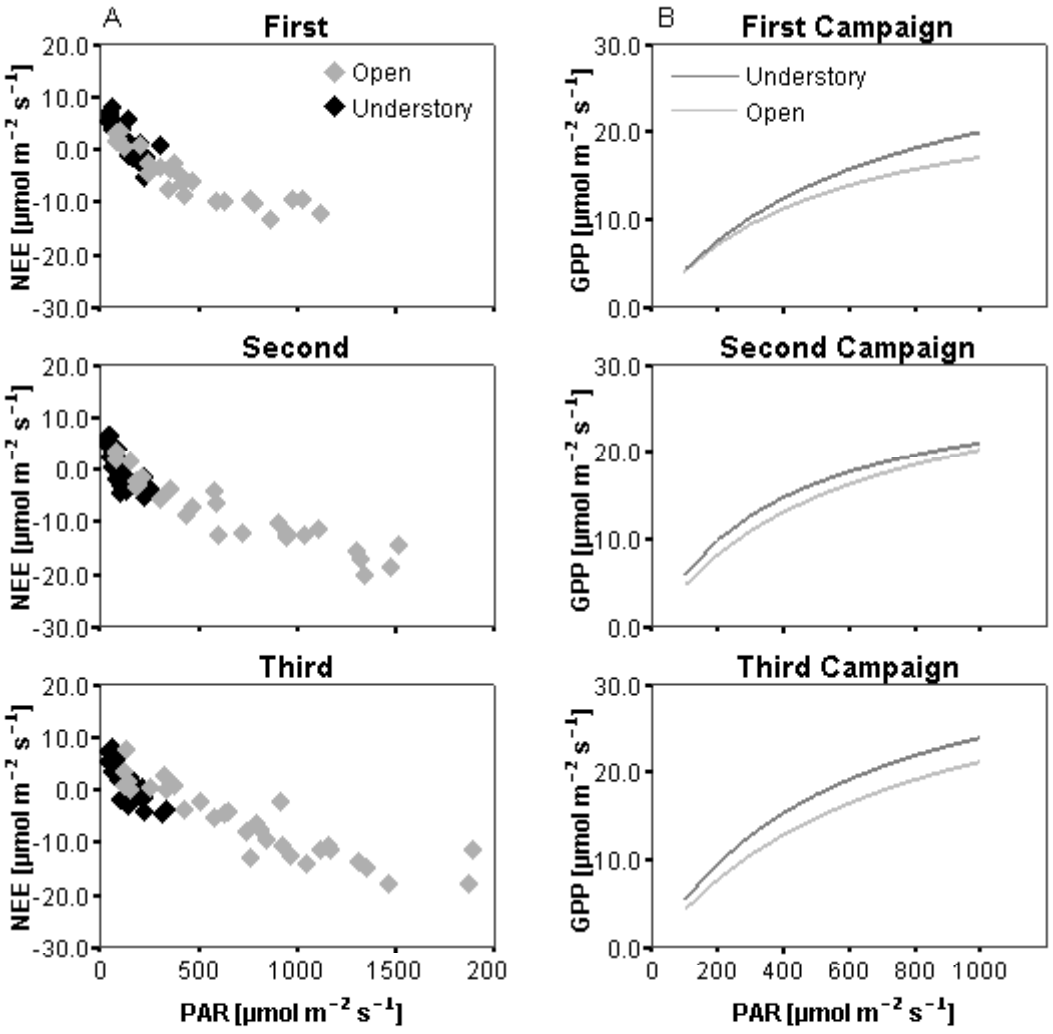


Figure 3.2.7.a shows the pattern of NEE light response in both understory and open locations. For all campaigns, slightly more negative values for NEE are exhibited at the understory locations as compared to open locations, at least over the range in PAR that is observed under trees. The differences are, however, quite small. Lower values mean more CO_2 uptake. The hyperbolic light response model (Fig. 3.2.7.b) predicted similar results for both locations, indicating slightly larger GPP values at understory sites (but not significant). Nevertheless, this is made up at open locations by the higher available PAR

Table 3.2.2. Estimated model parameters during 3 campaigns on DOY 80, 90 and 102 respectively. Each site is averaged based on 3 plots.

No of Data	Alpha	Beta	Gamma	R^2	Site	Management	Campaign
44	0.05	33.72	7.53	0.78	U	Ungrazed	1
44	0.05	26.17	5.89	0.96	O	Ungrazed	1
56	0.08	29.24	6.99	0.82	U	Ungrazed	2
46	0.06	31.80	7.08	0.95	O	Ungrazed	2
55	0.06	38.21	8.62	0.86	U	Ungrazed	3
48	0.05	37.44	10.99	0.93	O	Ungrazed	3
38	0.03	23.09	3.64	0.82	U	Grazed	1
31	0.04	34.03	6.03	0.88	O	Grazed	1
50	0.03	20.61	8.28	0.75	U	Grazed	2
63	0.04	43.56	14.68	0.89	O	Grazed	2
37	0.05	23.76	9.78	0.86	U	Grazed	3
40	0.03	49.20	13.59	0.84	O	Grazed	3
U=Understory,			***O=Open***				

Tables 3.2.3. Statistical analysis of model parameters in open and understory locations.

Open & Understory

Variables	Sum of Squares	df	Mean Square	F	Sig.
Gamma [µmol m-2 s-1]	53.43	1	53.43	8.35	.01
GPPmax [µmol m-2 s-1]	8.41	1	8.41	.36	.55

over certain periods of the day. Comparing the predicted model parameters between the locations showed a significant difference among campaigns (Fig.3.2.9, Table 3.2.3) in gamma. Thus, the larger R_{eco} values in the open location must be explained through higher soil temperature, higher aboveground biomass and perhaps differences in species composition. Figure 3.2.8.a and b show seasonal changes in soil respiration and a strong relationship between R_{eco} and soil temperature in both locations, indicating a stronger dependency at open sites. Figure 3.2.8.b explains the differences in R_{eco} among the two sites (understory and open) in the fenced location.

Fig. 3.2.8. (a) Comparison of ecosystem respiration (γ) in two location within 3 campaigns on DOY 80, 90 and 102 respectively and (b) relationship between soil temperature (10 cm depth) and R_{eco} during the third campaign (DOY 102).

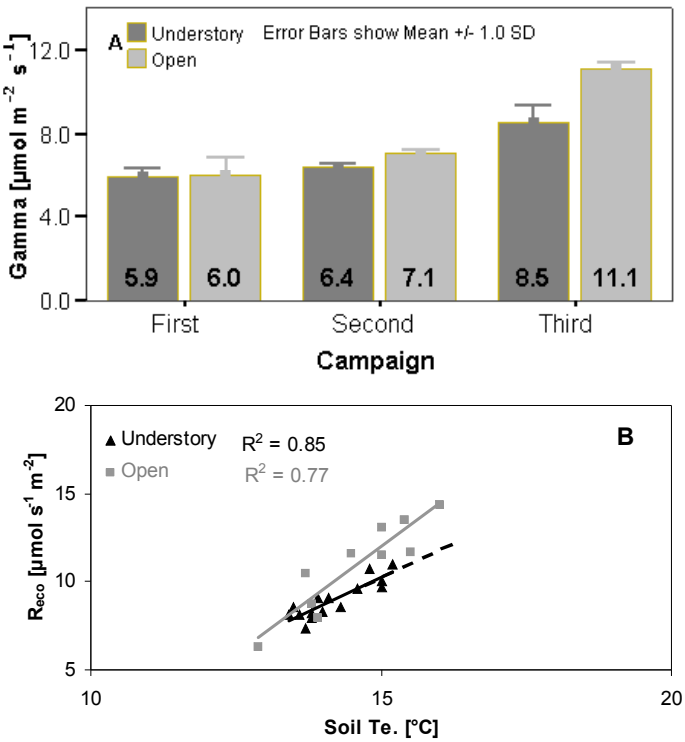
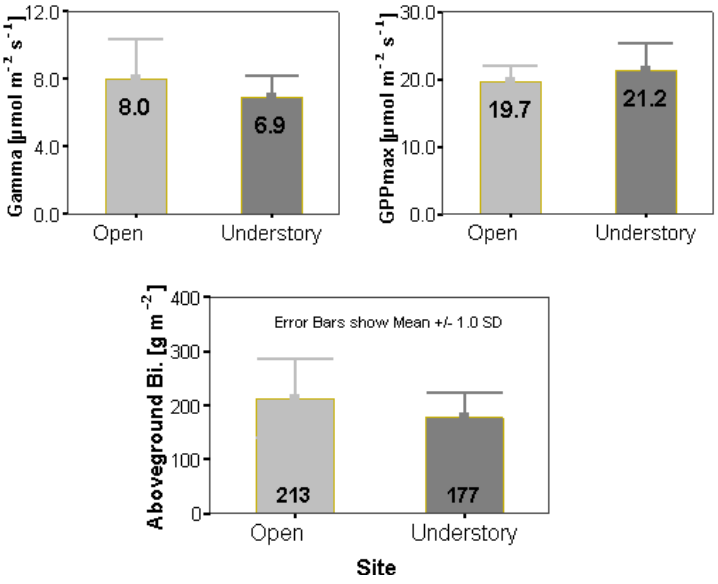


Fig. 3.2.9. Comparison of mean GPP and ecosystem respiration as gamma, considering measurements of all 3 campaigns on DOY 80, 90 and 102, respectively, and of aboveground biomass observed during the last campaign in understory and open locations during the growing season in 2006.



3.2.3.Effects of grazing

3.2.3.1 Grazing influences on seasonal patterns of biomass and nutrient distribution

Seasonal accumulation of above- and below ground biomass in grazed and ungrazed locations in the open and understory sites are shown in figure 3.2.10. Aboveground biomass in ungrazed was larger than in grazed locations. Averaged over the campaigns, there were 122 vs. 177 in understory and 192 vs. 219 g m^{-2} in open sites at the grazed and ungrazed locations, respectively. Root biomass showed a similar pattern to the aboveground biomass, with larger root biomass in ungrazed location in both sites. Foliar N concentration in understory and open sites showed a different pattern, with the ungrazed location in the understory having lower values compared to shaded grazed locations. In the open sites, ungrazed locations exhibited larger foliar N concentration during all campaigns (Fig. 3.2.11). Foliar C concentration in both grazed and ungrazed locations showed similar patterns. However, ungrazed locations had higher C concentrations. Root N and C concentration in ungrazed locations were higher (Fig.3.2.12), and differences between ungrazed and grazed locations were significant. Tables 3.2.4 shows the level of significant differences between these parameters at different sites.

Differences were also observed in soil N and C concentrations (Fig. 3.2.13), where % soil N and C in grazed sites within the first layer (0-7 cm), were larger than ungrazed areas. The difference between open and understory in the first layer (0-7 cm) was more remarkable, with high concentration of N under the trees. No significant differences were observed in % C and N concentrations in the 8-12 cm soil layer for the grazed and unglazed locations in the understory but significant differences was found in the open site, as shown in Table 3.2.5.

Fig. 3.2.10. Seasonal accumulation of above- and belowground biomass in grazed and ungrazed locations in understory and open sites during the growing season in 2006. Number of plots in each sample was three. Bars indicate standard deviation.

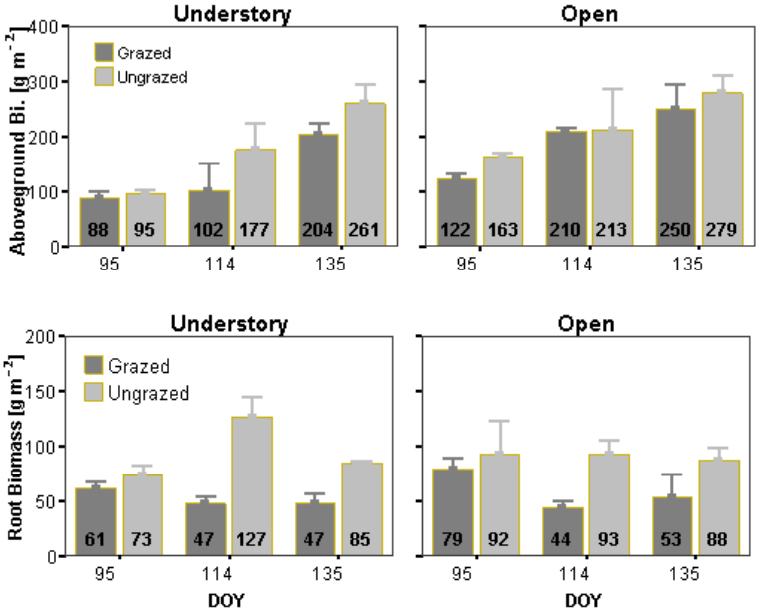


Fig.3.2.11. Foliar nitrogen and carbon concentration in grazed and ungrazed locations in understory and open sites during the growing season in 2006.

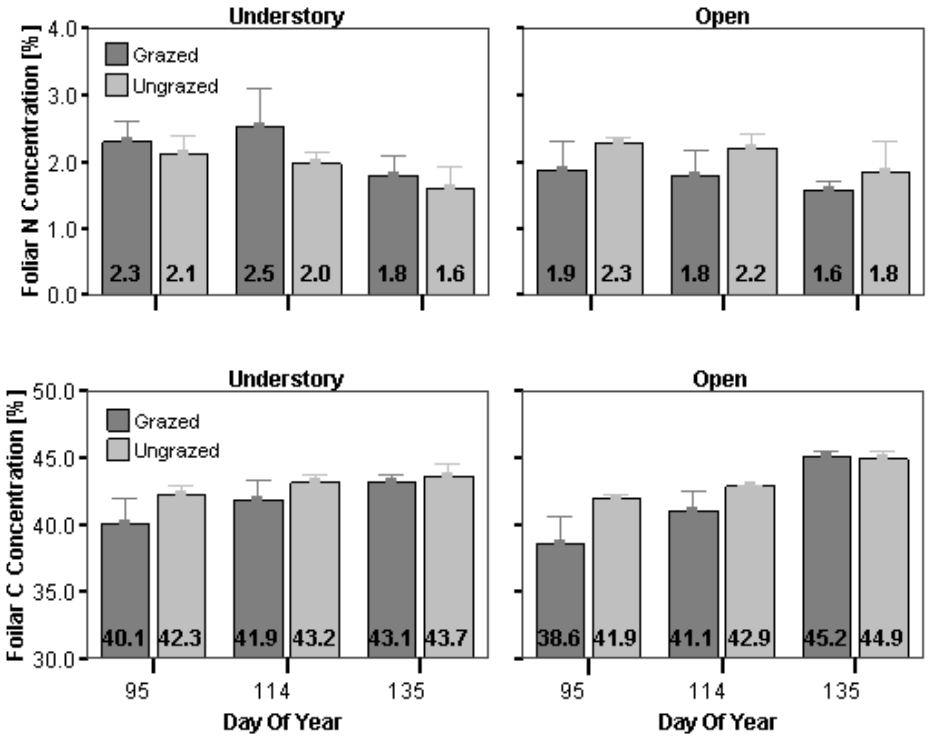


Fig.3.2.12. Comparison of root nitrogen and carbon concentration in grazed and ungrazed locations in understory and open sites during the growing season in 2006

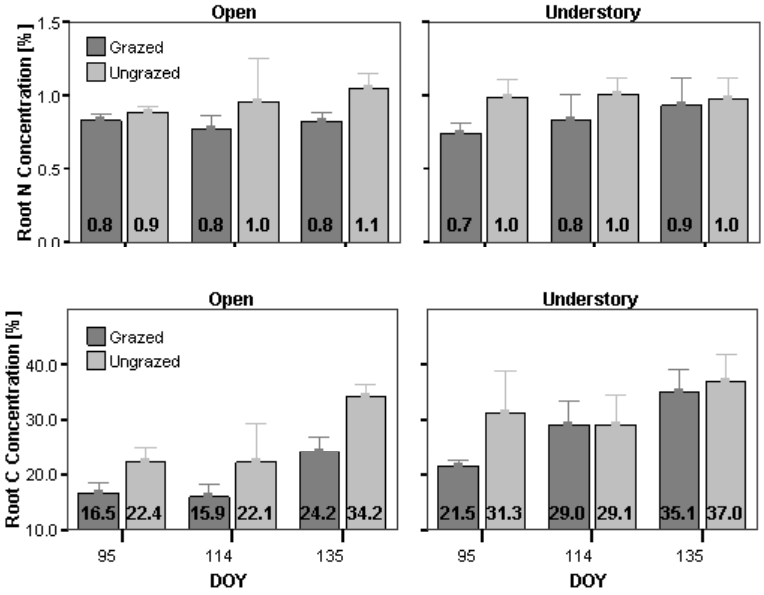


Table 3.2.4. Statistical analysis of biomass, nitrogen concentration and carbon content in grazed and ungrazed locations and for understory and open sites during the growing season of 2006.

Grazed and Ungrazed_Understory

Variables	Sum of Squares	df	Mean Square	F	Sig.
Aboveground Bi. [g m-2]	16833.66	1	16833.66	3.27	.08
Foliar N Concentration [%]	.57	1	.57	3.87	.06
Foilar C Concentration [%]	10.82	1	10.82	6.83	.01

Grazed and Ungrazed_Understory

Variables	Sum of Squares	df	Mean Square	F	Sig.
Root N Concentration [%]	.104	1	.104	4.54	.04
Root C Concentration [%]	34.917	1	34.917	.87	.36
Root Biomass [g m-2]	11470.080	1	11470.080	37	.00

Grazed and Ungrazed_Open

Variables	Sum of Squares	df	Mean Square	F	Sig.
Aboveground Bi. [g m-2]	10972.890	1	10972.890	4.76	.05
Foliar N Concentration [%]	.388	1	.388	3.50	.08
Foilar C Concentration [%]	11.929	1	11.929	1.77	.21

Grazed and Ungrazed_Open

Variables	Sum of Squares	df	Mean Square	F	Sig.
Root N Concentration [%]	.110	1	.110	6.31	.02
Root C Concentration [%]	245.401	1	245.401	6.85	.02
Root Biomass [g m-2]	9801.191	1	9801.191	2.71	.12

Fig.3.2.13. Soil nitrogen and carbon distribution in grazed and ungrazed locations during growing season in 2006.

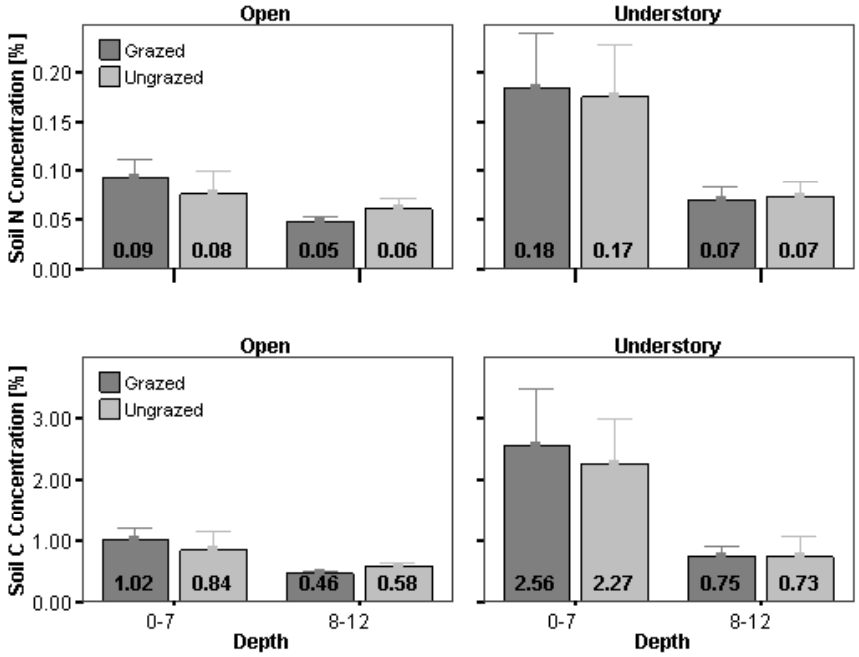


Table 3.2.5. Statistical analysis of soil nitrogen and carbon distribution in grazed and ungrazed locations in the understory site

Grazed and Ungrazed_Understory

Variables	Sum of Squares	df	Mean Square	F	Sig.
Soil N Concentration [%] 0-7	.000	1	.000	.12	.74
Soil C Concentration [%] 0-7	.307	1	.307	.42	.53
Soil N Concentration [%] Total	.000	1	.000	.03	.86
Soil C Concentration [%] Total	.090	1	.090	.43	.52
Soil N Concentration [%] 8-12	.000	1	.000	.33	.57
Soil C Concentration [%] 8-12	.002	1	.002	.04	.85

Grazed and Ungrazed_Open

Variables	Sum of Squares	df	Mean Square	F	Sig.
Soil N [%] 0-7 cm	.000	1	.000	1.08	.36
Soil C [%] 0-7 cm	.052	1	.052	.84	.41
Soil N [%] 8-12 cm	.000	1	.000	3.54	.13
Soil C [%] 8-12 cm	.022	1	.022	8.21	.05
Total Soil N [%]	.000	1	.000	.04	.86
Total Soil C [%]	.002	1	.002	.08	.79

3.2.3.1. Grazing Influences on net ecosystem CO_2 exchange

The analysis of ecosystem CO_2 exchange follows the same methodology as applied in section 3.2.2.3. Results of daily course of net ecosystem CO_2 exchange (NEE) in two sites consisting of grazed and ungrazed locations in open grassland and understory on individual days of each campaign measured using both light and dark chambers are presented in Figure 3.2.14. Results show significant influence of grazing on the quantity and pattern in NEE at both sites, especially in understory.

The relationship (R^2) between estimated and observed flux data, considering all campaigns at the different locations ranged between 0.85-0.95. Values for the parameters α, β, and γ for all measurement days derived from the model, are shown in Table 3.2.2. Net ecosystem exchange (NEE), was separated into its major components, namely gross primary production (GPP) and ecosystem respiration (*R*eco) via the general equation: GPP = *R*eco − NEE, and deriving Reco from gamma. Model predictions of ecosystem GPP responses are shown in figure 3.2.15. PAR was varied from 0-1000 μmol m^{-2} s^{-1} to determine the relationships for GPP vs. and PAR in different sites. The results show GPP-light response curves of different plots selected for the measurements during three field campaigns.

Grazed and ungrazed locations in understory showed different GPP values as well as different slopes. Ungrazed location in the understory showed higher GPP while respiration was similar in the both locations (Figure 3.2.15.a and 3.2.16.a). In the open site, there were no significant differences in GPP between grazed and ungrazed locations. However; respiration in grazed location was higher than at ungrazed locations (figure 3.2.15.b and 3.2.16).

Table 3.2.2.7 shows the level of significance for differences between grazed and ungrazed locations throughout three campaigns. Differences between GPP in grazed and ungrazed locations at the understory sites were significant ($p<0.06$) but not significant at the open sites. Open sites showed more respiratory loss (R_{eco}) in comparison to the understory (Fig. 3.2.17).

Maximum GPP (at the PAR_{1000}) in ungrazed and grazed locations at understory sites were 21.2 and 14 μmol m^{-2} s^{-1} respectively. Ungrazed location also accumulated more

biomass compared to the grazed locations (Figure 3.2.17.c). GPP_{max} in grazed and ungrazed locations at open sites were 18.7 and 19.7 µmol m^{-2} s^{-1}, respectively.

Fig. 3.2.14. Net ecosystem CO_2 exchange lights response curves, constructed based on data obtained from the light and dark chambers in understory and open sites within three campaigns during DOY 80, 90 and 102

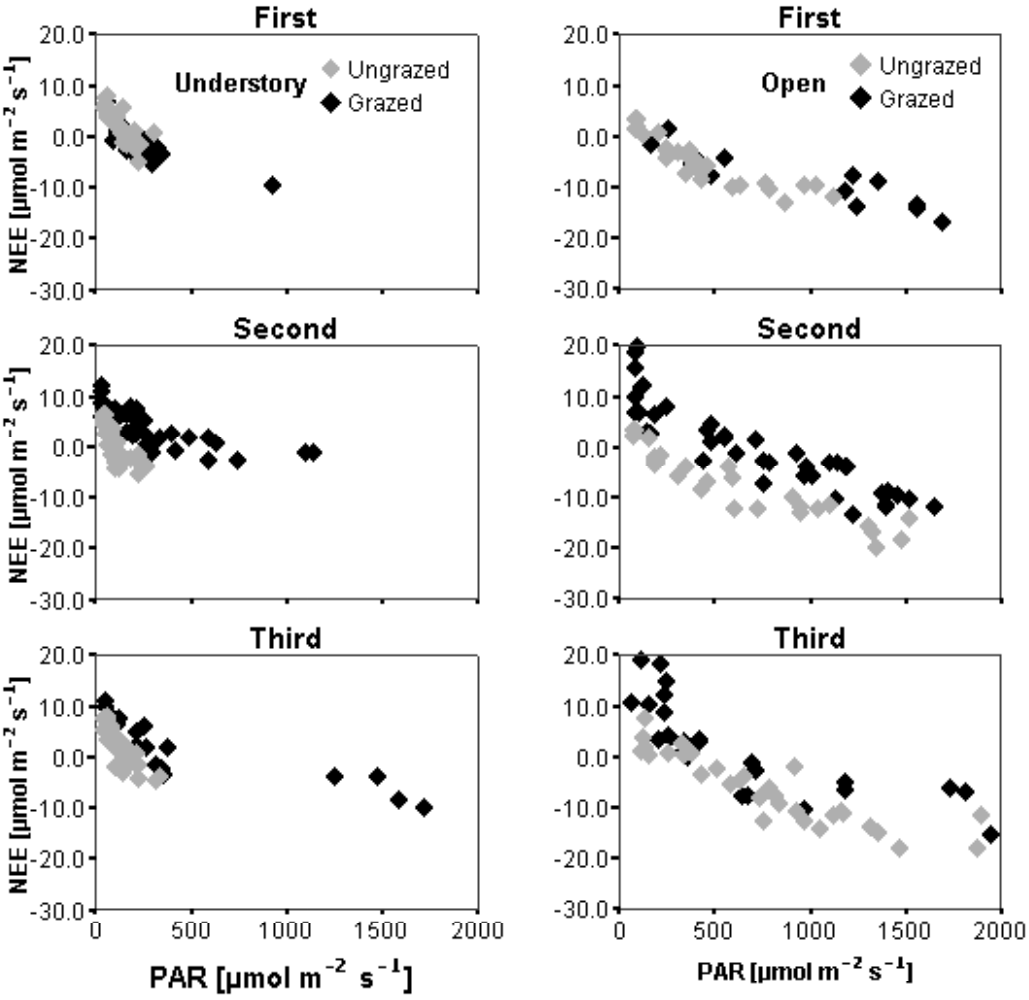


Fig. 3.2.15. GPP light response curves in grazed and ungrazed locations in the understory and open grassland as determined from the hyperbolic light response model, during three campaigns on DOY 80, 90, and 102 respectively.

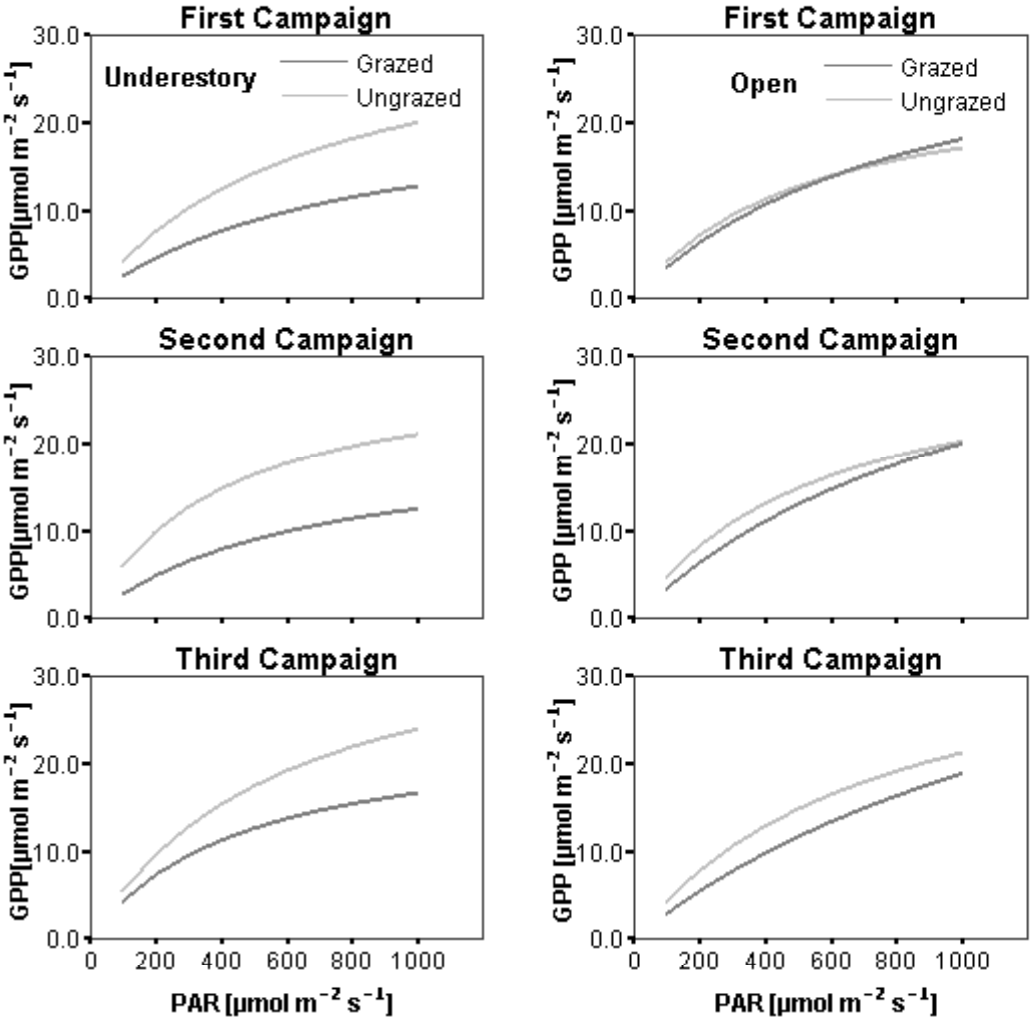


Figure 3.2.16. Comparison of γ within three campaigns occurred on DOY 80, 90 and 102 in grazed and ungrazed locations at two sites. The figures indicate time-dependent differences in ecosystem respiration.

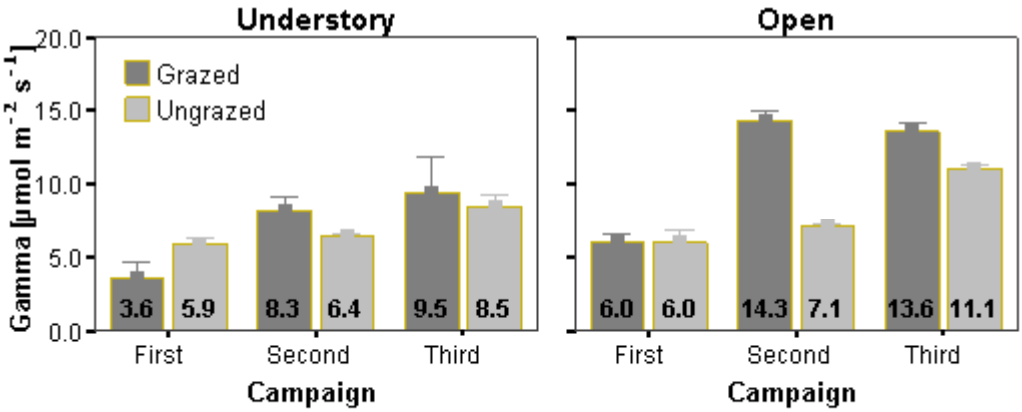


Table 3.2.7.Statistical analysis of model parameters, showing significant differences between two graze and ungrazed location in the understory and open sites

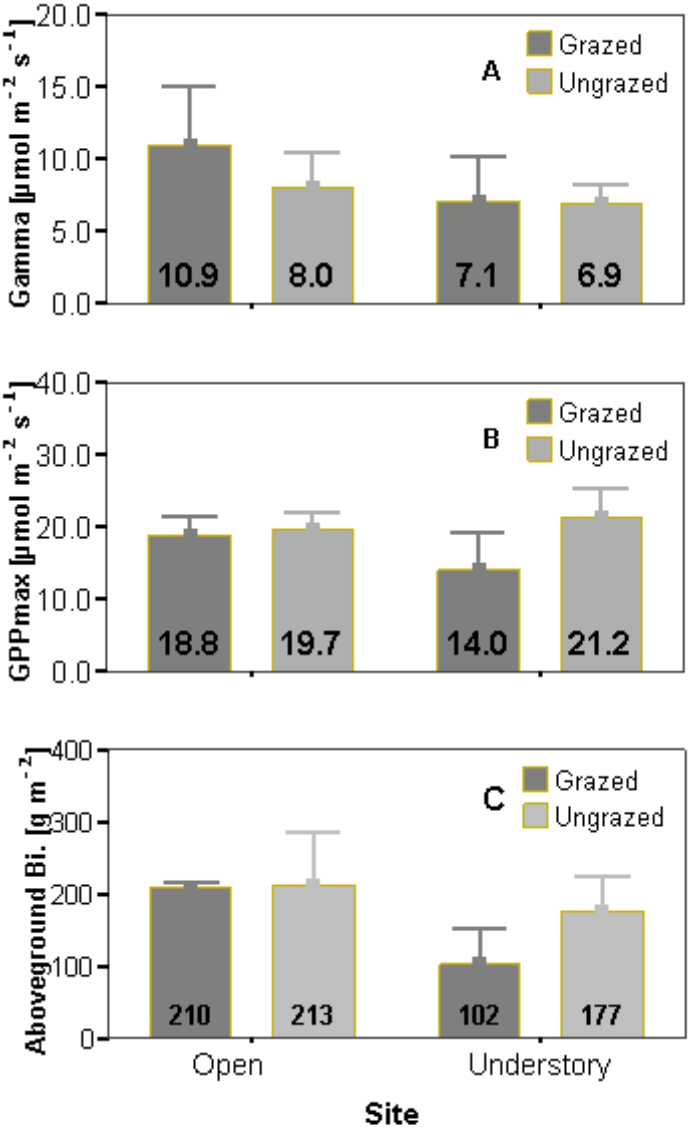
A-Grazed & Ungrazed_Open

Varibales	Sum of Squares	df	Mean Square	F	Sig.
Gamma [µmol m-2 s-1]	35.55	1	35.55	3.24	.09
GPPmax[µmol m-2 s-1]	3.18	1	3.18	.51	.49

B-Grazed & Ungrazed_ Understory

Variables	Sum of Squares	df	Mean Square	F	Sig.
Gamma [µmol m-2 s-1]	.09	1	.09	.02	.90
GPPmax[µmol m-2 s-1]	232.63	1	232.63	11	.00

Fig.3.2.17. Comparison of ecosystem respiration (γ), GPP throughout measurements and aboveground biomass in last campaing (DOY 102) in grazed and ungrazed locations at both open and understory sites.



3.3. Controlled experiments in artificial grassland with dominant temperate grassland species

3.3.1 Soil moisture and precipitation during study period

The purpose of the study was to examine how changing soil moisture conditions would impact plant functioning in temperate grassland ecosystems. This was facilitated by using semi-controlled conditions, since most of the European temperate ecosystems, including the experimental site in Grillenburg, only occasionally experience extreme fluctuations in rainfall. The study is, however, quite important in order to consider how temperate locations may respond to shifts in climatic conditions.

Species were utilized that are found both in European and Iranian temperate grasslands for these experiments. Since it is still not clear, whether changing climatic conditions will result in increased or decreased precipitation in the Iranian temperate regions, response to both extremes were examined. Figure 3.3.1 shows soil moisture [% volume] at 12.5 cm depth and precipitation during manipulations, as well as recovery after subjecting the grasses to extreme drought and heavy rainfall events. . Mean values and standard errors are shown.

3.3.2. CO_2 flux measurement

Results from the two communities (grass and grass-herbs) in three treatments (control, drought, heavy rain) during the third campaign using chambers and estimates of gas exchange according to the rectangular hyperbolic light response model are shown in figure 3.3.2. R^2 ranged in all cases between 0.85-0.95. Model parameters derived from this relationship from data collected during three campaigns are provided in Table 3.3.1. The table indicates model parameters and the relationship between observation and estimated data (R^2) within the three campaigns.

α is the initial slope of the light response curve and an approximation of the canopy light utilization efficiency (μmol m-² s-1), β is the maximum CO2 uptake rate of the canopy (μmol m-² s-1), γ is the average daytime ecosystem respiration (μmol m-² s-1) and NEE-max is CO_2 uptake estimated based on the model at 2000 μmol m^{-2} s^{-1} PAR.

Fig.3.3.1. Soil moisture and precipitation during the study period, Numbers 1 to 3 indicate end of gas flux measurement campaigns and date of biomass harvests (June, July, September). Grey bars show precipitation sums over 10 day periods for the weather manipulations in comparison with ambient conditions in 2005 (control) and the long term mean precipitation 1961-2000 (data: German Weather Service Station Bayreuth). The black horizontal indicates timing of the weather manipulations.

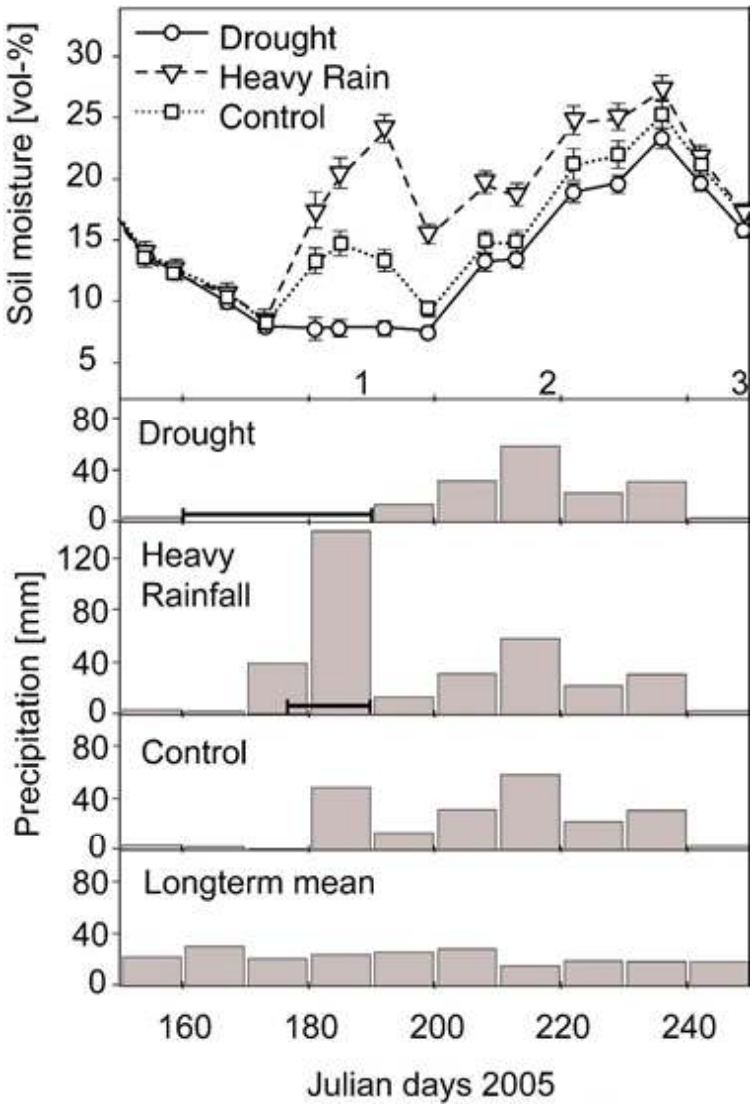
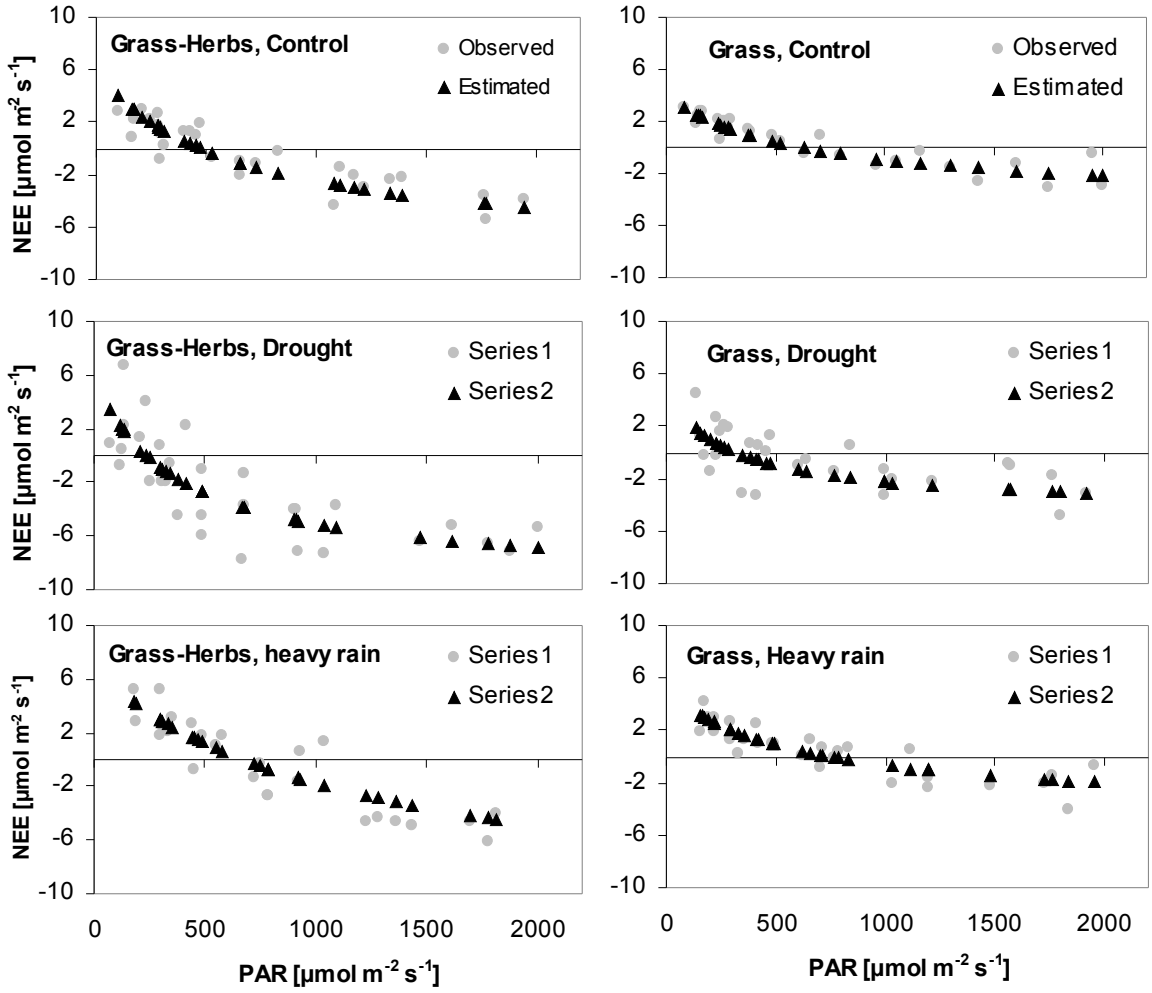


Fig 3.3.2. Comparison of CO_2 flux data obtained from the chamber measurements and estimates by the hyperbolic light response model in the two communities and three treatments during the third campaign.



3.3.3 Effects of extreme weather events on net ecosystem exchange and aboveground biomass and the role of the species composition

Carbon fluxes were significantly altered by the drought manipulation compared to the control with an increase in the light utilization efficiency (α) by 58 % ($p<0.05$) as well as an increase in maximum CO_2 uptake rate (β) by 14 % ($p<0.05$, Figure 3.3.3). The respiration term (γ) showed no significant effects from manipulation (Table 3.3.1).

Table 3.3.1 Parameters and the quality of the fit for the empirical light response model. Shown are mean values, standard error for each parameter, and mean r².

Data	α	β	γ	SE α	SE β	SE γ	R^2	NEE-max	Community	Treatments	Campaign
46	0.01	13.20	5.00	0.003	2.45	0.33	0.85	-3.76	Grass-Herbs	Control	Jun.
49	0.01	17.66	4.57	0.002	4.08	0.37	0.85	-5.60	Grass-Herbs	Drought	Jun.
41	0.01	25.03	5.49	0.002	5.42	0.34	0.92	-6.86	Grass-Herbs	Heavy Rain	Jun.
49	0.04	8.63	3.66	0.015	0.96	0.43	0.87	-4.10	Grass	Control	Jun.
41	0.05	7.09	3.05	0.037	1.20	0.59	0.84	-3.59	Grass	Drought	Jun.
40	0.02	8.25	3.50	0.006	1.20	0.36	0.86	-3.10	Grass	Heavy Rain	Jun.
40	0.03	19.39	6.25	0.004	1.87	0.35	0.94	-8.05	Grass-Herbs	Control	Jul.
37	0.03	21.14	5.88	0.004	2.51	0.42	0.93	-9.12	Grass-Herbs	Drought	Jul.
35	0.04	22.73	7.45	0.008	2.10	0.61	0.92	-10.63	Grass-Herbs	Heavy Rain	Jul.
45	0.02	10.33	3.94	0.004	1.07	0.25	0.90	-4.43	Grass	Control	Jul.
41	0.03	10.82	5.03	0.005	0.79	0.26	0.94	-3.95	Grass	Drought	Jul.
57	0.05	8.60	4.94	0.023	0.82	0.32	0.84	-3.03	Grass	Heavy Rain	Jul.
62	0.02	12.10	5.84	0.004	1.24	0.23	0.87	-3.81	Grass-Herbs	Control	Sep.
60	0.04	14.98	5.89	0.008	1.42	0.35	0.86	-6.80	Grass-Herbs	Drought	Sep.
60	0.02	18.22	6.82	0.003	3.46	0.31	0.85	-4.84	Grass-Herbs	Heavy Rain	Sep.
59	0.01	8.07	4.02	0.002	0.87	0.15	0.87	-2.14	Grass	Control	Sep.
61	0.03	8.83	4.58	0.008	1.01	0.28	0.86	-3.12	Grass	Drought	Sep.
66	0.02	9.19	5.04	0.003	1.22	0.20	0.83	-2.01	Grass	Heavy Rain	Sep.

Furthermore, no significant changes were found for heavy rainfall in any of the three parameters of the NEE light response curve model.

Maximum uptake capacity (GPPmax) was 15 % higher in the drought manipulation than in the control over time ($p<0.05$). Again, no significant effect was found for heavy rainfall (Figure 3.3.4). Significant effects were found for drought in parameter α and βand for diversity level in parameter β and γ according to Mixed Models ($p< 0.05$).

Aboveground biomass production did not show significant reactions to the applied extreme weather manipulations ($p>0.05$; Figure 3.3.5a). However, Leaf Area Index was 39 % higher in the drought manipulation as compared to the control over time ($p<0.05$; Figure 3.3.5b). The ratio between reproductive and vegetative biomass was shifted towards less reproductive and more vegetative growth following the drought manipulation (simplified mixed model: $p<0.05$). This difference was not apparent during the manipulations in June, but became stronger over time, and was significant after the

end of the manipulation (Figure 3.3.5.c). Integrated results over the three measurement times showed the ratio between reproductive and vegetative biomass decreasing by 57% in the drought manipulated plots (Figure 3.3.5.c). Significant effects between weather manipulation and control or between the two species compositions according to Mixed Models ($p < 0.05$) are marked with asterix. Mean values and standard errors are shown.

Fig.3.3.3. Light response curves of NEE in experimentally manipulated grassland communities of two diversity levels during and after simulation of extreme weather events.

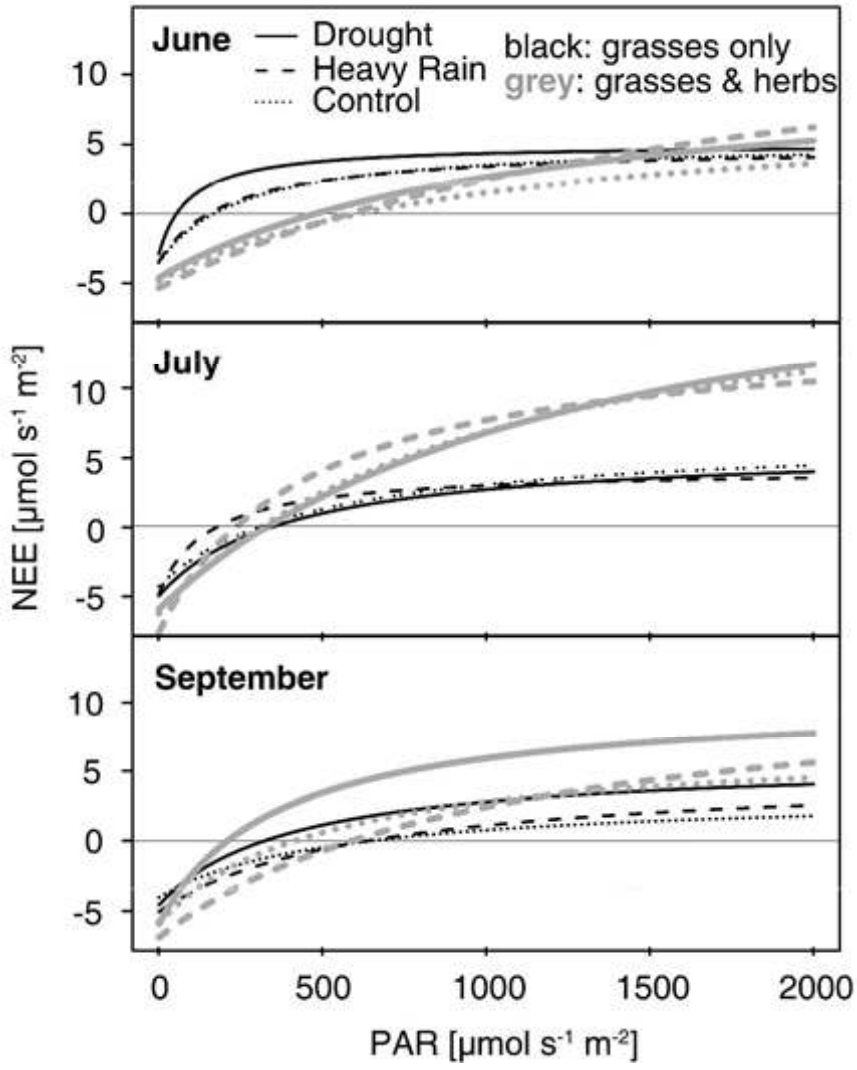


Fig.3.3.4. Maximum uptake capacity (GPPmax) in the experimental grassland communities separated by weather manipulations (left) and species composition (right).

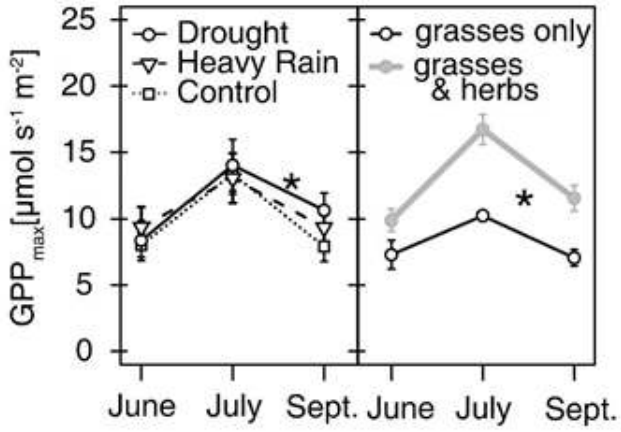
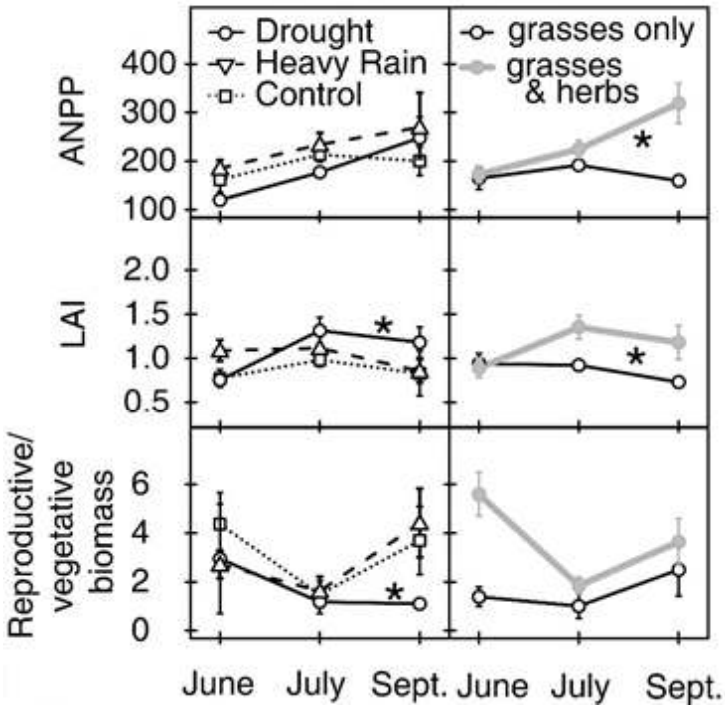


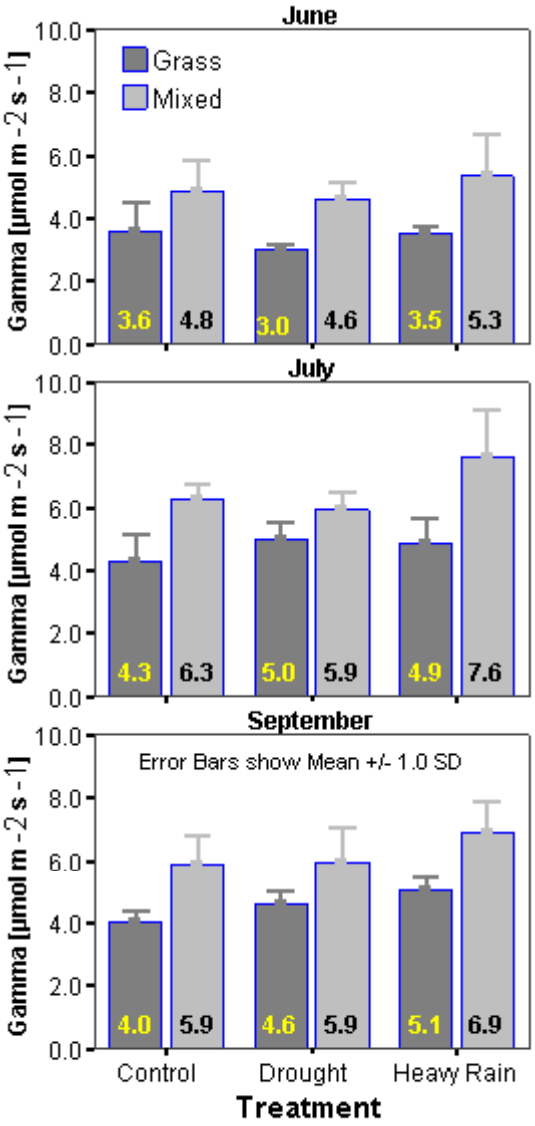
Fig.3.3.5. Aboveground stand development over time separated by weather manipulations (left) and species composition (right). The figure shows aboveground biomass in g m^{-2} (a), Leaf Area Index (b), and the ratio between reproductive and vegetative biomass.



The observations indicated no significant interaction between weather manipulations and species composition. Significant effects between weather manipulations and control or between the two species compositions according to Mixed Models ($p < 0.05$) are marked with an asterisk. Mean values and standard errors are shown.

The two species compositions differed in their responses, with the more diverse community showing an increase in maximum CO_2 uptake rate (β) by 110 % compared to the less diverse community (mixed model: $p<0.05$). This is a more significant increase than the one found for the drought manipulation. The more diverse community also exhibited a 40% increase in the respiration term (γ) as compared to the less diverse community (mixed model: $p<0.05$, Figure 3.3.6). Ultimately, maximum uptake capacity (GPP-max) was 12 % higher in the more diverse community (mixed model: $p<0.05$; Figure 3.3.4). Aboveground biomass production and LAI were consistently higher in the more diverse community (for both parameters mixed models: $p<0.05$; Figure 3.3.5). Species composition did not alter the response to extreme weather manipulations, as the mixed models did not detect any significant interaction between diversity level and weather manipulations.

Figure 3.3.6. Comparison of Reco (γ) in two communities, separated by weather manipulations during three campaigns



Chapter 4
Discussion and Conclusions

4.1. Temperate grassland

Long-term climate records of Grillenburg show that the region receives adequate amounts of rainfall throughout the year. With a mean annual amount of 756 mm, vegetation growth and development is apparently seldom limited by soil moisture (1971-2000, Tharandt weather station). Low temperatures and PAR, however, restrict growth during mid-spring until early autumn, when otherwise favorable conditions prevail (Humphreys et al., 2005; Kato, et al., 2006). Although the amount of rainfall received during the study period was well above the long-term annual mean (798 mm), plant growth and biomass development only began in April, a time when PAR and temperature were favorable for plant growth (Figure 3.1.1). Rapid biomass development recorded after day 120 was attributed to rapidly increasing light and temperature, which stimulate plant biological activities (Long et al., 1994, Daepp M., et al., 2001). Environmental conditions, especially rainfall, light and temperature, have been shown to influence shoot development rate and plant growth (Pontes L. 2007, Lantinga et al., 2002). Biomass development generally followed seasonal patterns of daily temperature and PAR.

Plant growth and development depends partly on accumulated reserves of carbon, which in turn is regulated by the seasonal variations in climatic conditions (Suyker A., et al., 2003; Penuelas J., et al., 2007). The amount of carbon reserves, which determine the overall growth in any productive season is determined by the photosynthetic capacity of the plants, the available leaf area, plant respiration and the existing climatic conditions. Seasonal changes in ecosystem CO_2 fluxes are closely related to the changes in physiological activity of the ecosystem and occur in response to meteorological conditions. In the temperate regions, the period for carbon uptake can be restricted by temperature, light and moisture conditions, as well as by leaf phenology (Keeling et al., 1996; Myneni et al., 1997; White et al., 1999; Jackson et al., 2000).

Patterns of biomass accumulation reflected LAI development (Fig.3.1.3), strongly supporting the role of leaf area development in overall productivity. Similar conclusions have been reached at by Flanagan et al., 2002; Xu and Baldocchi, 2004; Byrne K.A., et al., 2005 for grassland ecosystems. Disturbing the LAI distribution, as is the case in

managed grasslands (Figure 3.1.5.), therefore has consequences for ecosystem productivity. The Grillenburg results showed that mowing reduced LAI as well as biomass, with subsequent impact on overall carbon uptake capacity of the grassland ecosystem (Figure 3.1.10). Seasonal changes in LAI, were similar to those of live biomass (Figure 3.1.3). Significant differences between the two sites occurred in leaf biomass, rather than in leaf area. For example on DOY 238 and 313, aboveground biomass, were 148, 88 (in cut site) and 326, 140 g m^{-2} (in uncut site) respectively, while their LAI were 2.03, 1.17 (cut site) and 3.22, 1.76 (uncut site) respectively that shows larger SLA (Specific leaf area = LA/Leaf mass) in the cut location. This can be attributed to either re-growing of fresh biomass and young tissues in the cut location or senescence in the uncut site, or both. LAI declined to below 0.45 m ^{2}m $^{-2}$ at the end of the active growing period. Previous studies have shown the effects of cutting on quality of leaves. Cutting reduced development of stems and spikes (Smethan, 1990), and resulted in higher leaf-stem ratio (Boval et al., 2002). Cutting frequency affects the productivity of forage plants, partly through changes to their morphological development (Binnie and Chestnutt, 1991; Vinther, 2006; Santis et al., 2004; Turner et al., 2006)

Apart from leaf area development, biomass productivity in grass communities also depends on root development, since roots have a role in nutrient and water uptake (Bokhari and Singh, 1974; McDuff and Jackson, 1992). Development of the root biomass is influenced by soil moisture, favorable soil temperature and carbon from the aboveground photosynthesizing plant mass (Grayston et al., 1996). The pattern of root biomass development reflected seasonal variations in temperature and rainfall as well as the growth of the aboveground biomass (Fig 3.1.4), with peak root mass being experienced between DOY 180 and 210, a time when soil temperature was highest. Seasonal changes in total live belowground biomass mainly reflected climate, with the growing season being limited to the warmer and wetter part of the year.

As long as soil moisture (Figure 3.1.2) and nutrient (Figure 3.1.6-8) conditions remain favorable, root development should have a close relationship with aboveground green biomass (Teixeira et al., 2008; Holly et al., 2001). Practices, such as mowing that reduce the aboveground shoot structure, must influence root biomass development as found in other ecosystems (Georgiadis et al . 1989; Mazancourt et al . 1998). The Grillenburg

results show that the below ground biomass at the uncut site reached a peak of 1032 g m^{-2} in early summer and sharply decreased thereafter. Peak belowground biomass accumulation coincided with the reproductive stage, a time when plant uptake capacity was declining. Decline in root biomass thereafter could depend on the decreasing photosynthesizing surface area as a result of leaf senescence and also on resources being used for reproductive structures such as seeds.

One would expect a different response pattern in managed grasslands, since cutting keeps the grass leaves young and fresh and this may also influence roots (Fig. 3.1.5). The results show that root development in the managed plots reflected changes in PAR and soil temperature, reaching a maximum of 1205 g d m^{-2} soon after the first cutting. Although regeneration of green biomass occurred after the cuttings, this did not have any influence on root biomass development, and root biomass continued to decline after the reproductive stage was reached, similar to the unmanaged sites. Becker et al. (1997) found that root growth of two grass species (*Stipa tenuis* and *Piptochaetium napostaense*) was not reduced when they were defoliated early, rather than late in the growing season. Guitian, et al. (2000) found that mean root biomass did not vary between plants species, but was significantly ($P< 0.0001$) affected by defoliation treatment, declining with increasing intensity of defoliation.

Leaf nutrient content distribution over the year resembled the fluctuation in aboveground biomass, e.g. maximum tissue N (7.68 g m^{-2}) was recorded in early May (Figure 3.1.8.a) coinciding with peak green biomass (maximum foliar accumulation). Seasonal variation of leaf N concentration in the enclosure site showed a peak value in the beginning of the growing season and steadily declining thereafter, until the mid-growing season when the vegetation was in the flowering phase. After flowering, N remained stable until the end of the growing season. The results are consistent with other studies, indicating highest values in the early growing season with a gradual decease until the end of growing season when the nutrient concentrations appeared to become diluted as the aboveground dry matter increased, and the canopy senesced. (Clark et al., 1990; Beal et al., 1997; Vinther 2005).

Cutting the aboveground biomass influenced foliar N concentration, causing the biomass to attain another peak value of N in the mid-growing season, when the uncut site showed its lowest value (Figure 3.1.8). Cutting induced enhancement of aboveground N concentration, which came as a result of increased demand for N in the regenerating fresh tissue after the cut. These results are consistent with those from other mowed grassland sites (Vinther 2005; Soussana et al., 2004; Schaffers 2002; Green & Detling, 2000; Turner et al. 1993; Wallace et al., 1982)

At a given harvesting date, the differences in nutritive value of forage grasses may occur because of differences in phenological stage (Bruinenberg et al., 2002). Comparison of seasonal pattern of leaf N concentration shows that decreases in leaf N % due to senescing of the vegetation, was delayed by cutting of the aboveground biomass (Fig.3.1.8). This can lengthen the vegetative growth phase for grasses, digestibility of leaf is highest in the vegetative stage and declines with advancing phenological stage (Smethan, 1990).

Biomass development depends on the long-term accumulation of carbon, which occurs through photosynthetic uptake of atmospheric CO_2 (Lawlo , 2002). Ecosytem carbon budget is therefore determined by the balance between C uptake during photosyntehesis and C loss during respiration (Lawrence, et al, 2002). Monitoring of CO_2 exchange in the ecosystem provides a mechanism by which biomass development can be assessed both in the short and long-term. Assessment of NEE during 2004 showed its dependence on environmental factors, mainly PAR (Figure 3.1.13) and temperature, (Figures 3.1.1-2). Thus, seasonal pattern of CO_2 assimilation in this ecosystem strongly agrees with the observed pattern of biomass accumulation (Figure 3.1.11).

In a system where soil moisture (Figure 3.1.1) and nutrients (Figures 3.1.6-8) are not limiting, carbon exchange processes are influenced most by factors other than soil moisture and nutrient characteristics (Suyker and Verma, 2001; Davison et al., 2000). For Tharandt, light and temperature interact in a particular way so as to determine ecosystem production. During active plant growth, peak ecosystem NEE during the day is strongly dependant on the amount of radiation received while the total carbon fixed depends on the duration and level of peak assimilation rates (Byrne , et al., 2005, Figures 3.1.10-12).

Similarly, peak NEE is influenced by the respiratory capacity of the ecosystem, which in turn is influenced by temperature (Bahn , et al., 2006; Davison et al., 2000; Hanson et al., 2000). The Grillenburg results showed a strong influence of temperature on both NEE and R_{eco} (Fig. 3.1.10-11), as already reported for similar ecosystems (Jacobs et al., 2007; Yuste et al., 2004; Flanagan et al., 2002; Vukicevic et al., 2001; Suyker et al., 2001). Thus the overall ecosystem production (biomass) is determined by an interaction between the two processes, namely assimilation and respiration on the one hand and the climate environment consisting of light and temperature on the other (Flage et al., 2002).

Available photosynthetic surface area and nutrient availability in the soil must also influence the uptake capacity. The results showed that changes in soil N were insignificant throughout the growing period of the grass (Figures 3.1.9-10) and hence nutrition was regarded as non-limiting to plant growth and development. It was therefore expected that as long as climate conditions were conducive for photosynthesis, the main determining factor on ecosystem assimilatory capacity would be the available leaf area. This was monitored through LAI. A strong relationship existed between NEE and LAI, an indication of the role played by LA in determining ecosystem production (Figure 3.1.11). The relationship between CO_2 uptake and LAI has been reported elsewhere (Byrne et al., 2005; Xu and Baldocchi, 2004; Flanagan et al., 2002).

Standardizing seasonal NEE with parallel LAI measurements should provide a strong indication of physiological changes that accompany plant growth during the season as long as radiation remain comparable. Similar features could be derived from respiratory capacity of the system, which dictates the eventual carbon reserves. Thus dividing ecosystem respiration rates with paralleled biomass over the season should equally provide valuable information on plant physiological changes.

Fundamental changes in the landscape pattern and ecosystem structure and functioning can affect the spatial structure of plant canopies, species composition and physiology, nutrient availability and in consequence the biosphere-atmosphere CO_2 exchange, which in turn may feed back on the atmospheric CO_2 concentrations (Cernusca et al., 1998). After first cutting, both GPP and R_{eco} sharply declined and ecosystem started to act as

source of CO_2. Thereafter, (10-15 days later) the grassland was again assimilating carbon caused by re-growing of the aboveground biomass.

R_{eco} increases resulting from seasonal increase in temperature (fig 3.1.11), influence on GPP rates because the physiological response of plant and soil respiration to changes in temperature and moisture can vary throughout a season (Luo et al., 1996; Tjoker et al., 2001). Therefore a large part of GPP increases on DOY 205 is contributed to raising the ecosystem respiration during this period.

During winter and early spring daily rates of net carbon exchange were low and the balance between NEE and respiration (R_{eco}) was nearly zero. However, there were appreciable carbon losses, which were predominant over carbon uptake especially in early winter, and this condition continued till early spring (Figure 3.1.2). Thus, carbon losses were predominant during the low temperature periods. Cumulative rates of NEE showed the grassland during 2004 overall acted as sink of carbon dioxide by sequestrating –260 g m^{-2} $year^{-1}$ CO_2.

Significant reduction in NEE as a result of cutting attributed to the reduced photosynthetic surface area (Fig 3.1.11). Immediately after harvesting, there is a period of approximately 2 weeks during which there is net emission of CO2, but this is reversed to net uptake, when new tissues are formed Similar results have been reported by Jaksic et al., (2006). Net CO_2 evolution after cutting is due to root and soil respiration (Michael B., et al., 2006; Jaksic et al. 2006; Rogiers et al., 2005; Ronald et al., 2000; Green et al., 2000). Hence, there is strong evidence that rates of plant production and soil respiration are linked processes.

Unlike the mowed plots, the uncut locations despite having higher aboveground biomass had lower GPP (Figure 3.1.5.b and 3.1.15) likely the result of leaf aging and senescence as well as to partial shading by overlapping leaves. Studies conducted elsewhere reported that photosynthetic carbon uptake of *Lolium perenne* increased by 44% after a harvest (Ainsworth et al., 2003), coinciding with leaf area development. Increased foliar N after the cutting could also enhance the leaf photosynthetic capacity and consequently result into larger GPP. This supports the view that there is a strong association between foliar N concentration and photosynthetic capacity, regardless of whether variation in N arises

from variation in rate of N supply and differences in leaf age (Connor et al., 1993; McCullough et al., 1994b; Vos and Van, 1998) or differences in illumination among leaves by mowing (Vos J., et al., 2005).

4.2. Mediterranean grassland

Daily maximum air temperatures increased steadily, with increasing radiation input, from 11.6 °C in early March to 31.1 °C in late-May (Figure. 3.2.1.b), while precipitation and soil moisture decreased and the most part of vegetation withered in early-June (Figure 3.2.1). This is typical of the montado region as demonstrated in the long-term climate analysis of the study site (Pereira et al 2008). Plant growth and development are strongly regulated by the climatic variables particularly the interaction between temperature and precipitation (Aires et al. 2008a). Previous studies show that despite favorable soil moisture between October and April, growth of the herbaceous layer only commences in March, when air temperature is conducive for growth (Aires et al. 2008a and b). The measurements in the herbaceous layer component of the montado were therefore, confined to the period between March and May, when active growth and development occurs (Pereira et al. 2008, Aires et al. 2008a and b, Otieno et al. 2008).

Spatial heterogeneity created by the scattered trees is likely to create spatial differences in microclimatic and soil moisture conditions in the montado as found in other similar ecosystems (Franco & Nobel 1988; Callaway 1992; Maestre et al. 2003; Lorena et al. 2005). In this study, differences in radiation distribution upon the landscape are expected, which could significantly influence soil moisture and temperature, impacting plant growth and overall ecosystem functioning. This was the case as demonstrated in figure 3.2.2 b, with the understory location experiencing lower soil and air temperatures and higher soil moisture than the open locations. Such differences are likely to result in differences in plant composition and ecosystem responses between the two locations (Casper and Jackson 1997; Lorena et al., 2005). The Evora results however, revealed no influence on the herbaceous layer production, with no significant differences in total biomass production between the two locations (Figure 3.2.3.a). Callaway et al. (1991) found that herbaceous biomass under individual *Quercus douglasii* canopies in oak

woodlands in California varied significantly, with much higher biomass in the understory than in the open locations.

Although facilitative interactions have been demonstrated in a broad range of ecosystems (Callaway and Walker 1997; Holmgren et al., 1997), most evidence comes from ecosystems where plants are exposed to severe stress. It is suggestive that a positive effect of trees on understory production and plant composition is determined by the mean annual precipitation and temperature. Previous studies showed a negative effect of trees under higher precipitation, e.g. in regions with more than 500 mm mean annual precipitation, *Quercus douglasii* canopy cover reduces understory forage yield compared to open grassland but may increase yields in drier regions (McClaran and Bartolome 1989). In this study, less influence of overstorey on the herbaceous layer productivity can be explained by high total annual precipitation (730 mm), leading to reduced facilitation. According to Holmgren et al. (1997), Fernandez et al., (2003), positive and negative interactions may occur simultaneously and the net effect of tree canopies on the understory may easily shift from facilitative to competitive, or conversely, when conditions change.

Trees, regardless of understory biomass, add considerable amounts of nutrients to the soil beneath their canopies (Figure 3.2.1) and have the potential to facilitate understory production. Although there was no significant difference in total biomass accumulation between the two locations, evidently, there was higher root biomass accumulation in the understory in April, a time when active growth was recorded in the herbaceous layer. Such increase in root biomass would be interpreted as a response to limiting soil moisture or soil nutrients and is could improve nutrient uptake (Braziotis and Papanastasis, 1995; Papanastasis et al., 1995; Garcia et al., 1999, Zarovali et al., 2007; Jackson et al., 1990).

Analysis of soil N concentration revealed higher soil N under the trees than in the open locations (Figure 3.2.6). Since similar biomass was recorded in both locations, tissue N concentration in the herbaceous understory should be higher than in the open locations. This was however not the case (Figure 3.2.5), bringing into question the role of favorable microclimate and soil conditions under the trees on ecosystem productivity. Most of the N nutrient was concentrated within the top 0-7 cm soil layer, suggesting that it comes

from mineralization (Federer et al., 1983; Rey et al., 2005). Trees have been regarded as pumps of mineral nutrients, transporting nutrients from deeper to upper soil layers (Callaway, et al., 1991; Rice, 2000; Gallardo, 2003). This could contribute to the higher N concentration under the trees as compared to the open location. Equally, more surface litter in the understory, originating from trees, could cause this significant difference in N and C between the open (26%) and understory (32.5%) locations (Figure 3.2.5).

The fate of this nutrient pool and its contribution to ecosystem productivity is, however, not clear. Otieno et al. (2007) suggested a net transport of nutrients from the understory to the surrounding open locations. This could be a possible conclusion since there was no supporting evidence that it was taken up by the understory vegetation. Callaway et al. (1991) found that soil nutrient deposition in *Q. douglasii* woodlands was much higher under tree canopies compared to the open grassland. However, most of the nutrient deposition was in organic form and not immediately available for plant uptake. (Callaway et al., 1992). In a similar ecosystem in Spain, a higher concentration of organic matter and essential nutrients for plants (N, P and K) was found under the *Quercus ilex* holm oak canopy. However, all nutrients showed different patterns of spatial distribution. N is the only nutrient whose spatial pattern greatly coincided with soil organic matter and its values showed a high spatial structure at the sampling scale, with the highest values coinciding with tree canopy projection (Gallardo, 2003, Rice, 2000). Several studies have shown that both herbage production and nutritive value decrease as the tree canopy or density increases (Braziotis and Papanastasis, 1995; Papanastasis et al., 1995; Garcia et al., 1999, Zarovali et al., 2007).

Biomass production is the result of carbon uptake (NEE) by the available green plant material. Although NEE was limited by light intensity in the understory (Figure 3.2.7), model projection of GPP showed no difference between the understory and the open locations in their assimilatory capacities. This was in agreement with results from biomass production (Figure 3.3.3). Previous studies conducted in the same area show similar results, indicating lack of differences in seasonal patterns of NEE between the oak woodland and the grassland (Pereira et al., 2007). One would anticipate higher NEE in the understorey vegetation due to higher soil moisture and soil nutrients in these locations compared to the open (Fig.3.2.6). However, such advantages are cancelled out by the low

light intensities received in the understory compared to the open locations. Thus, low maximum assimilation rates during the day as a result of low light intensity leads to reduced overall production (Jackson, et al. 1990; Callaway, et al., 1991; Klemmedson, 1991; Dahlgren, et al., 1997). Although the understory vegetation can remain active for longer and continue to photosynthesize (Franco & Nobel 1988; Callaway 1992; Maestre et al. 2003; Lorena et al. 2005).

Significant differences, however, occurred between the two locations in ecosystem respiration (R_{eco}) during the third campaign (DOY 122). Such differences could be attributed to differences in soil temperature (Figure 3.2.2.a), soil moisture (Figure 3.2.2.b) and belowground biomass (Figure 3.2.3). Strong correlation between respiration and soil temperature have been reported in different ecosystems (Lloyd and Taylor 1994; Davidson et al., 1998; Raich et al., 2000; Xu and Baldocchi, 2004; Hunt et al., 2004; Jones et al., 2006). All these studies have shown that increases in ecosystem respiration are associated with increasing soil temperature, since higher temperatures during the growing season enhance plant and microbial activity leading to higher soil respiration. Soil temperature in the open locations was always 3 °C higher than in the understory. Results of this study suggest a linear sensitivity of soil respiration to temperature in both locations (Figure 3.2.8.b), supporting this line of argument.

Significant differences in daily soil respiration because of phenological changes have also been reported elsewhere (Fu, et al., 2002). These findings show significant increases in respiration from vegetative to flowering stage. Increased respiration in the open compared to shade locations could as well be due to phenological differences among species in the two locations. The Evora results showed that the vegetation in the open locations reached maturity 2-3 weeks earlier than understory. While the open vegetation were at the end of their flowering stage, those in the understory were still in the vegetative stage and consequently the vegetation in open demonstrated higher respiration at the reproductive stage much earlier (Xu and Baldocchi 2003). Differences in species functional-group composition can also influence soil respiration since vegetation affect soil respiration by influencing soil microclimate and structure, the quantity and quality of detritus supplied to the soil and the overall rate of root respiration (Raichi et. al., 2000). This implies that environmental heterogeneity related to microhabitat could play a key

role in spatial patterns at broad spatial scales, and consequently in the dynamics of the distribution and establishment of herbaceous species (Madrigal, et al., 2007).

Grazing had a significant influence on above- and belowground biomass, resulting in overall reduction in the total biomass accumulated during the season (Fig.3.2.10). Depending on the grazing intensity, different results have been reported on the role of grazing on grassland production. For example, Mohdkheir, et al. (1999) reported a decline in the above and belowground biomass under grazing compared to ungrazed locations in a Mediterranean grassland. Intensive grazing management through short rotation is widely believed to increase grassland forage production by ensuring more uniform forage removal and allowing a recovery period (Gammon 1978). Large herbivores have a critical effect on the structure and function of grassland ecosystems leading to alteration in composition and aboveground productivity of the vegetation (McNaughton, 1983; Milchunas and Lauenroth, 1993).

The Evora results showed that grazing increased foliar N concentration and decreased foliar C in the understory locations in the montado, showing significant differences between the grazed and ungrazed sites (Figure 3.2.13). Lower foliar N concentration at the open grazed compared to the ungrazed locations could be explained by lower soil N concentration in the open locations. (0.09 and 0.18 in open and understory locations respectively). Herbivory has often been reported as contributing to higher tissue nutrient (N and P) concentrations in annual (Ruess and McNaughton, 1987; Hiernaux & Turner, 1996) and perennial grasses (Holland and Detling, 1990; Holland et al., 1992; Bardgett et al., 1998).

Root N and C concentrations declined in grazed locations in both the understory and open. It has been hypothesized that decreased root biomass and root C allocation in heavily grazed grasslands is an important link between long-term grazing and soil microbial processes in perennial grasslands. In a similar ecosystem in Spain (Dehesa) soils under the oak canopy showed higher values of soil organic C and total-N within the top 5 cm of the soil profile (Gallardo A. et al., 2000). Different authors have described nutrient enrichment under tree canopies for semiarid ecosystems (Belsky A.J., 1994; Jobbagy, E.G., 2001; Moreno G., et al., 2007). Their findings agree with the results of

this study, which showed significant differences in soil N and soil C concentration in the shallow soil layers of both the understory and open locations. Organic and mineral components in soils located under the tree canopies were higher partly due to leaf shedding and litter fall in spring and summer (Gallardo and Merino, 1992). However, there were no significant differences in soil N concentration between two sites (grazed and ungrazed) in both locations, because grazers on the one hand decrease soil N concentration by grazing the vegetation and on the other hand, they add minerals to the soil through urine and dung deposition. (Whitehead, 1995, Gallardo and Merino, 1992).

No differences between grazed and non-grazed treatments were found. C and N concentrations were, however, higher in all soil horizons beneath the oak canopy compared to the open grasslands (Dahlgren R.A. et al., 1997). Soil C concentration was lower in the grazed sites than in the ungrazed sites and this was more pronounced in the open location. This was an indication that soil C was increased by grazing, caused by a higher annual shoot turnover and a redistribution of C within the plant–soil system as a result of changes in plant species composition (LeCain *et al*. 2002 and Reeder & Schuman, 2002)

Depending on the location under consideration (open vs understory), grazing influenced CO_2 exchange processes differently. There were no significant differences in NEE and GPP between grazed and ungrazed sites in the open locations, while remarkable differences occurred in the understorey (Figure 3.2.14). NEE in the grazed location in the understory were significantly lower than in the ungrazed location (Figure 3.2.15). Grazing could lead to compensatory plant growth due to increased plant CO_2 assimilation per cm^2 tissue (e.g., McNaughton 1976; Frank and McNaughton 1993; Milchunas and Lauenroth 1993; LeCain et al. 2000, Risch A.C. et al., 2006), however changes in plant species composition, influenced by grazing could alter aboveground biomass, LAI, and thus CO_2 assimilation capability (Schuman et al. 1999; Schoenecker et al. 2002). Other studies have found no significant difference in NEE between grazed and non-grazed areas (LeCain et al., 2002; Wilsey et al., 2002; Risch & Frank, 2006). Aires et al., 2008 reported that grazing exerted only short- term negative impact on daily NEE in same place. In the summer, grazers often congregate under the trees to spend the hottest part of the day. This causes damage to the vegetation under the trees, resulting in reduced

assimilatory capacity (Joffre 1988) as observed in figure 3.2.14-15. One might predict that the large differences between herbaceous vegetation in the understory location at grazed and ungrazed sites is more due to animal trampling than to the grazing effect. Ecosystem respiration at the grazed site in both locations open and understory was higher than those occurred at the ungrazed sites particularly in the open location (Figure 3.2.16-17). This finding is generally consistent with the results reported from different grazed grassland ecosystems which state that higher respiration in grazed areas is due to increases in soil microbial biomass, resulted in higher respiration in lightly grazed area (Bardgett et al., 2001; Frank and Groffman, 1998; Frank et al., 2000; Le Roux et al., 2006). Therefore, the peak in soil microbial biomass in lightly grazed grasslands might support the idea that response to intermediate levels of herbivory is related to more rapid circulation of nutrients (McNaughton, 1985; Deyr et al., 1993; Loreau, 995; Bardgett et al., 2001).

4.3.Controlled experiments on dominant temperate grassland species

Impact of changing precipitation on productivity of temperate herbaceous species

Shifts in climatic conditions will likely impact on the performance and stability of the temperate grasslands with consequences for their ecosystem service delivery (Wessel et al. 2004). Shifts in climatic conditions are likely to lead to increases or decreases in precipitation amounts and distribution depending on the geographical location of the region under consideration (IPCC 2007). Assessing the impact of climate change on temperate grasslands that are currently receiving adequate precipitation amounts with limited or no annual drought cycles can only be achieved through controlled experimentation, either in the greenhouses or in semi-controlled field experiments as designed for the University of Bayreuth Botanical Garden. Controlled experiments in the botanical garden, aimed at examining the impact of rainfall shifts, showed that drought altered carbon fluxes in the grassland systems without significantly changing the aboveground biomass production (Figure 3.3.2-3 and 3.3.5). GPPmax and the uptake capacity were increased after inducing the drought (increased values for $\alpha.\beta$ (see Figure 3.3.4). The respiration term (γ) was, however, not affected by drought. Increase in

photosynthesis was attributed to increased assimilatory efficiency with the aim of conserving water (Aranda 2005).

A possible consequence of drought in these grass species could be an increase in Leaf Area Index (LAI) due to shifts in aboveground carbon allocation from reproductive to vegetative structures. Such responses have been described for grazing ecosystems in Europe (Jaremo et al., 1996; Van der Graaf et al., 2005), and is generally discussed as plant compensatory growth (McNaughton, 1983). Another possible explanation would be a shift in species composition and relative importance of each species due to the applied drought. Assessment of species composition on the study site showed that species composition changed due to the drought manipulation (Kreyling et al., in press). There was an increased dominance of the more drought tolerant species, with a higher water use and carbon assimilatory capacity. Evidently, *Lotus corniculatus*, a dominant legume herb in the temperate grasslands, exhibited significantly higher die-back when subjected to water stress, thus creating room for the more adapted grass species. As grasses generally have higher LAI than herbs (Schmid, 2006), such a change in community composition may add to the observed increase in LAI without change in total biomass in the present study.

Although aboveground biomass remained relatively unchanged by drought despite significant increase in CO_2 assimilation (Figure 3.3.5), an increase in root biomass in the drought treated plants was expected, since increases in NEE mean increased carbon fixation, which is then redistributed to the roots to improve soil water uptake either through increased root biomass or increased cell solute concentration (Thomas and James, 1999). Amiard et al. (2003) observed increases in fructan concentrations in grasses during water stress. Increased relocation of carbohydrates, particularly to the roots, was reported by Karsten and MacAdam (2001), Breda et al. (2006), and Hamidou et al. (2007). No significant shifts in root length were apparent in the botanical garden experiments (data not shown). However, plant roots contribute to soil carbon not only through their death and decomposition, but also by rhizodeposition resulting from exudation, mucilage production and sloughing from living roots (Vanveen et al., 1991; Reeder et al., 2001). So far, there are no hints as to where the additional fixed carbon after drought treatment has been stored. Even though carbon allocated to the root system

might be more stably sequestered (Jones and Donnelly, 2004), the long-term duration of such effects, the consequences to soil carbon pools, and the overall importance need to be further investigated. This is, however, difficult in the experimental design at the botanical garden, since the treatments and plant populations should be maintained over the long-term, limiting destructive studies.

Increases in NEE during drought has been reported for a cerrado ecosystem in Brazil (Miranda et al., 1997). Although these are systems that have adjusted to regular drought periods, the observations for temperate grassland species subjected to drought suggest a similar response. Miranda et al., (1997), observed that despite significant increase in NEE in the cerrado, during water stress, the ecosystem still had an overall carbon loss. This was attributed to high respiration rates resulting from stimulation of soil microbial community due to increased release of carbon from the roots into the soil (Craine, J. M., et al., 2001). The results in the current experiments, however, did not show such strong increases in respiration during drought manipulation (Figure 3.3.6), an indication that the fixed carbon during this period is immediately transformed into more stable pools. Interestingly, the effects of the drought manipulation on NEE became more obvious two months after the termination of the manipulations (Figure 3.3.2 and 3). This fact clearly illustrates that drought may have long-term implications on ecosystem functioning. Similar conclusions have been reached by White and Jentsch (2001) and Jentsch et al. (2007).

This assessment of temperate grasslands has been planned in terms of evaluating contributions to fodder production for animals and, thus, accumulation of aboveground biomass was of major interest. The results showed that both drought and flooding did not have significant impact on biomass production. It can therefore be implied that reduction or increase in precipitation of the imposed magnitude, resulting from possible climate change, may not pose serious implications for the productivity of these grassland ecosystems. Other experiments simulating drought by comparable methods in the field, but with more extreme manipulation intensity and duration, reported decreased productivity, e.g., Grime et al. (2000), Penuelas et al. (2004) and Kahmen et al. (2005).

It can be assumed that events which lead to a decrease in aboveground productivity can no longer enhance NEE, and an increase in frequency and magnitude of such events is predicted (Meehl et al., 2000b; IPCC, 2007), leading to conditions under which previously rare events happen in consecutive years or reach unprecedented extremity.

The findings in this study suggest that there could be thresholds or turning points, which will stimulate plant responses to environmental changes when such thresholds are exceeded. The findings are inconclusive and further investigations are needed, with more intense and prolonged stress treatments in order to derive more concrete conclusions. Increased NEE due to drought as obtained in this study must, therefore, be treated with caution, since different responses may occur when drought intensity exceeds the adaptive capabilities of the ecosystem (Karsten et al., 2001; Valladares et al., 2002). The interaction between several climate parameters may also influence the response of an ecosystem to a given treatment. For example, elevated atmospheric CO_2 concentrations, might reduce the vulnerability of grassland production to climatic variation and climatic change to some extent (Soussana and Luscher, 2007).

The heavy rainfall manipulation resulted in no significant changes in NEE or above ground biomass production. This is most likely due to the fact that the applied manipulation did not lead to longer periods of completely saturated soil as expected (Figure 3.3.1).. The results, however, are in agreement with those from a similar study reported by White et al. (2000), indicating that water treatment did not significantly alter absolute or relative productivity of the species consisting of three grasses and one legume.

Role of species composition

The results of the study showed a crucial role played by species composition in regulating carbon fluxes and ecosystem productivity (Fig. 3.3.2). The more diverse community exhibited higher potential for carbon uptake (β) as well as increased respiration (γ) (Table 3.3.1 and Figure 3.3.6). Net carbon sequestration seemed to increase substantially in the more diverse community, since GPP_{max} was 55% higher than in the grasses only community. However, the strong increase in aboveground productivity in the more

diverse community suggests that the net carbon uptake was transferred into aboveground biomass. Since the priority in these ecosystems is the provision of fodder, promotion of ecosystem diversity is a sure way of enhancing productivity and ecosystem sustainability (Beierkuhnlein and Nesshoever, 2006). Naeem et al. (1994; 1995) reported significant increases in community respiration at comparatively high diversity levels in grassland plant assemblages.

4.4 Comparison of temperate, Mediterrranean and artificial grassland response

Ecosystem descriptive properties

At the temperate grassland site in Grillenburg, biomass developed rapidly after DOY 120 and was maximal in mid-June (408 g m^{-2}, Fig.3.1.3), whereas at the Mediterranean site in Mitra, herbaceous green biomass increased much earlier, from March to mid-May. Biomass accumulation was maximal on DOY 135 (279 g m^{-2}, Fig.3.2.3). The relative rate of increase in biomass, however, is about the same, and similar to that found for many European grasslands after growth commenced (Li et al. 2008). In the case of the artificial grassland, a comparison is not possible, since they were established by plant transfer from trays and since sequential harvests were not possible. Maximum aboveground biomass in the plots was lower than in natural field conditions with values of ca. 200 g m^{-2}. In correlation with biomass differences at the study sites, maximum LAI was 5.5, 3.5 and 1.5 at Grillenburg, Mitra and in the botanical garden plots, respectively.

Considering the Figures 3.1.2 and 3.2.1, it is clear that there are different patterns in precipitation, temperature and PAR in temperate and Mediterranean grasslands. Nevertheless, biomass development in both generally follows the seasonal patterns of daily temperature and PAR, because environmental conditions, especially rainfall, light and temperature during the main growth periods are usually not extreme. The response of shoot development rate and plant growth to these factors has been extensively documented (Pontes L. 2007, Lantinga et al., 2002). We can assume that similar responses occurred as well in the artificial grassland communities.

Mean maximum aboveground foliar N concentration in the temperate grassland occurred in mid-May, coinciding with early growing season, with 3.4% nitrogen. In the Mediterranean grassland, foliar N concentration reached a peak value in early-April which was lower (2.3%) averaged over the stand biomass. The plant communities in the botanical garden experiments had foliar nitrogen of ca. 1.5 % in grasses and 2.7% in the legumes. For separate growth forms, the same concentrations were found in Mitra. Thus, nutrition of the plants appears to have been similar in Mitra and the botanical garden, and was less favorable than at Grillenburg, perhaps due to the coarse soil without humus at these two locations. Along with the extreme change in soil properties, root biomass was ca. 1200 g m^{-2} when assessed to 30 cm depth in Grillenburg, but only 100 g m^{-2} at Mitra. Sampling was not carried out in the permanent plots at the botanical garden. Obviously the contribution of legumes (which was high in Grillenburg) together with soil N supply are factors controlling biomass development and the final aboveground pool of N which determines carbon exchange. As in the case of foliar N, root N concentration was also lower in the Mediterranean grassland (ca. 1 %) than in the temperate grassland (1.5%).

Soils in cooler climates commonly have more organic matter because of slower mineralization (decomposition) rates (Bot and Benites, 2005). From the sampling that was possible, soil total N content was also similar in the botanical garden and in the Mitra plots (ca. 0.07%). In Mitra, higher soil N content occurred at the beginning of the growing season in shaded locations. In terms of available N in soil solution, it was low in Mitra (ca. 0.2 μmol g^{-1} soil) in early spring (Otieno et al. 2008), while it remained near 0.6 μmol g^{-1} soil throughout the season in Grillenburg. Thus, growth and development of biomass is sensitive to fluctuations in temperature and PAR, but the total biomass accumulation should be at a lower level in the Portuguese grasslands (as well as the botanical garden communities) due to greater nutrient limitation. Climate effect and management cause additional seasonal and spatial differences between these grasslands (Figures 3.1.2 & 3.2.1, and as discussed in 4.1 and 4.2). The effects of reduced water availability are discussed below.

Grassland ecosystem physiology

The pool of aboveground nitrogen in an ecosystem, especially in grasslands, may be seen as an indicator of physiological activity, particularly since large amounts of leaf nitrogen are invested in photosynthetic metabolism. Aboveground nitrogen is influenced by the accumulation of biomass, by nitrogen investments in individual organs (here of interest is the foliage), and species composition as it influences these investments. The aboveground pool of nitrogen at maximum development in Grillenburg was ca. 8 g m^{-2} (Fig. 3.1.6), while in Evora it was only 4 to 6 g m^{-2}. In the botanical garden, this was not assessed in order not to disturb the long-term plots, but aboveground nitrogen must have been even lower than in Evora, if we consider the information on biomass and leaf N concentration given above. NEE, model parameters and estimated GPP should be correlated with these changes in the aboveground N pool.

Measurements of NEE coinciding with peak biomass during the growing season showed differences between these grasslands in their assimilatory capacities, indicating that maximum amount of NEE at light saturation were ca. -25, -15 and -5 to -12 (depending on community composition) µmol m^{-2} s^{-1} in temperate, Mediterranean, and artificial grasslands, respectively. Model projection of GPP_{Max} provides values of ca. 30, 20 and 12 to 17 µmol m^{-2} s^{-1} for the same series of sites. After the first cut in Grillenburg, the aboveground biomass, N pool and LAI were lower, as were maxima for NEE and GPP, similar to the maxima observed in late spring in Mitra. Thus, in Grillenburg we have a progressive increase in N limitation on ecosystem physiology. However, it seems that Mediterranean grassland exhibits similar respiration (viewed from the model parameter γ) as found in Grillenburg. A similar result was reported by Flage et al. (2002) in a Mediterranean evergreen forest versus temperate forest ecosystem comparison. The cause is unclear at the present time.

Extreme weather events consisting of both; simulated drought and heavy rain treatments in temperate grassland during first year didn't change biomass accumulation, compared to that at the controlled site, but GPP_{Max} and the uptake capacity were increased after inducing the drought condition, most likely due to changes in vegetation structure which increase LAI. Respiration (γ), however not affected (Aranda 2005; Van der Graaf et al.,

2005; Jaremo et al., 1996; McNaughton, 1983). Our result showed that in cold temperate grassland with enough annual precipitation a short period of extreme weather events could not have a negative effect on production and CO_2 ecosystem exchange. We concluded that the NEE for this humid grassland ecosystem was not very sensitive to the variation in precipitation (cf. Jasic et al., 2006), even though soil water content was strongly reduced (Fig. 3.3.1) and led to strong short-term reductions in NEE. The role of water stress is, therefore, quite different in the temperate and Mediterranean grasslands. In temperate locations, the vegetation usually survives and recovers function in CO_2 uptake, while adapting in response to drought experience. In the Mediterranean site, drought play a role by simply limiting the active period, where response is sensitive to temperature and PAR controls.

It was shown that cutting frequency and grazing caused different effects on Mediterranean and temperate grassland. We found that cutting frequency in temperate grassland increased leaf N concentration and CO_2 assimilation. Similar findings have already been reported in the other studies (Michael et al., 2006; Jaksic et al. 2006; Rogiers et al., 2005; Ronald et al., 2000; Green et al., 2000). Cutting in Grillenburg also decreased ecosystem respiration. In contrast, in Mediterranean grassland, grazing had neither a positive nor a negative effect on carbon assimilation, but increased ecosystem respiration. However, grazing also caused increases in leaf N concentration along with decline in above- and belowground biomass.

Review of the hypotheses

In general, the hypotheses (section 1.5) are supported by the studies that were carried out. Nevertheless, Mediterranean and temperate grasslands were found to differ more strongly than expected due to nutrient availability, which depends on the prevailing higher temperatures, annual changes in water balance and possibly nutrient removal from the ecosystem in Mediterranean regions. The light response model allowed effective and additional comparison of the observed data, i.e., is a useful tool is describing grassland ecosystem differences. Differences in temporal patterns of stress and in their intensity, whether as extreme events or as a normal annual occurrences, must be further studied, since they do impact ecosystem CO_2 exchange, biomass development, and productivity.

These impacts are complex and must be examined further at natural field sites and in controlled experiments such as those carried out with artificial communities in the botanical garden. Furthermore, experiments must be designed that consider in greater detail the different responses of grassland species and communities of different composition. Community composition can lead to large changes in ecosystem response. Similarly, the study of cutting, grazing and management measures were shown to be very significant, and these must also be examined with greater attention.

4.5 The current study relative to similar ecosystems in Iran

The results obtained in experiments carried out in this thesis work are in agreement with and support conclusions from previous studies performed in Mediterranean and temperate grasslands in Iran. Since overgrazing is a big problem in natural grasslands of Iran, most research has been focussed on grazing systems, and improvement of vegetation quality (Mesdaghi, 1993; Moghadam, 1997; Hazell, et al., 2001). The botanical garden experiments demonstrate that influence of species selection on ecosystem function (potentially improving quality) can be examined in detail and explained, even though the observed responses may be quite complex and require a large time investment in order to accomplish an explanation.

Raiesi and Asadi, (2006) reported that no significant differences in soil organic C and total N concentration and C/N ratios were observed among three (overgrazed, frequently grazed and non-grazed) sites in a Mediterranean grassland in north-west of Iran. The findings in the montado near Evora (Mediterranean grassland) are similar. However, Raiesi and Asadi, (2006) found the grazed sites to exhibit greater respiration. This has also been reported by others (Sanadgol et al. 2003; Javadi et al. 2005). Intensive grazing sharply reduced below- and aboveground biomass, and plant diversity and caused soil degradation in different regions of Mediterranean and temperate grasslands of Iran. However moderate and late grazing increased palatability and foliar nutrient content of the vegetation (Mesdaghi, 1993; Moghadam, 1997; Chaichi 2000; Arzani et al. 2007).

In Mediterranean grasslands of Iran, the herbaceous layer beneath the trees is strongly influenced by the overstory layer (Mirzaei and Mesdaghi, 1996), particularly in southern

aspects and with steeper slopes. This might be due to the poor nutrient status and shallow soil depth in such areas, where the herbaceous species more greatly profit from influences of woody plants on microclimate and ecosystem heterogeneity as compared to similar gradients in other grasslands. Sheidaei and Nemati, (1978) indicated that soil nutrient content and soil moisture in the understory of trees were higher and showed more fertility in their profiles compare to the open areas.

However, there remains a lack of detailed information about the natural Mediterranean and temperate grasslands in Iran. In this sense, the results of the current study are very useful either to fill gaps in information or to provide a background concept for planning such detailed experiments. Despite wide applicability of the findings achieved in the current study, they cannot replace similar investigations in Iran, because of variability in the composition of the vegetation, the probability that these species possess unrevealed adaptations, and wide extent in distribution of Iranian grasslands along strong climate gradients (cf. section 1.2.1.3). There is an essential need and to experimentally investigate the natural grasslands of Iran, in order to identify management problems and determine the role they play with respect to global warming and in the context of climate change (Bordbar et al., 2004).

The effect of biotic and abiotic factors on CO_2 exchange, soil and biomass nutrient content and carbon sequestration in grasslands of Iran are all themes for which critical information is lacking (Reich & Eswaran, 2002). New initiatives on field studies and modeling are required in this region, in order to fill gaps in our knowledge on grasslands in a global context..

Chapter 5
Summary

Current projections indicate that global temperatures are likely to increase by 1.1 to 6.4 °C between 1990 and 2100 due to climate change. Expected temperature increases are attributed to increased anthropogenic greenhouse gas emissions, which lead to warming of the earth's surface and the lower atmosphere due to increased greenhouse effect. Arresting the escalation in atmospheric CO_2 levels requires that emissions into the atmosphere be significantly reduced and /or CO_2 withdrawal from the atmospheric pool must be stepped up. Plants, through carbon sequestration, play a significant role in the global carbon balance as sinks of carbon, withdrawing atmospheric CO_2 and converting it into assimilates and biomass during photosynthesis, translocation and storage.

The global estimates of the relative amounts of C in different ecosystem types suggest that grasslands probably contribute 10-30% of the total biosphere store, and that they play an important role in the biosphere–atmosphere exchange of major greenhouse gases. Temperate grasslands comprise approximately 32% of the earth's natural vegetation and about 20% of the land area in Europe. Mediterranean ecosystems occupy less than 5 % of the Earth's surface, yet they contain about 20 % of the world's flora, including important components in grasslands.

In the current study, the biophysical processes related to CO_2 exchange, biomass production and nutrient uptake and use in temperate and Mediterranean grassland ecosystems were comparatively studied. The work addresses the need to understand grassland ecosystem processes as they relate to productivity, carbon exchange and nutrient dynamics in detail, as well as how they relate to environmental shifts and existing or potential future management practices. The objectives of this study were to determine how seasonal changes in microclimatic conditions influence soil water and nutrient availability, and their impacts on bioproductivity of temperate and Mediterranean grasslands. Furthermore, the work has explored the role of ecosystem heterogeneity, species interactions and management practices with respect to CO_2 and nutrient exchange of Mediterranean and temperate grasslands.

Therefore, two sites were selected in Central Europe, consisting of a grassland (Grillenburg) to evaluate effects of management (cutting frequency) and a controlled experimental grassland (Botanical Garden of the University of Bayreuth), to assess the influences of normal and extreme weather condition on carbon exchange, productivity and nutrient dynamics. In the artificial experimental grasslands in the botanical garden, species diversity was varied and climate treatment effects were evaluated. Additionally, a man-made Mediterranean grassland savanna at Herdade da Mitra, Portugal was studied to evaluate the effects of climate, of management (grazing) and of distribution of trees (overstory) on herbaceous vegetation function and productivity. Measurements of net ecosystem CO_2 exchange, NEE, were carried out using closed chambers, while sampling of above – and below ground biomass and soil carbon and nutrient pools were carried out in the same plots. The measurements were conducted periodically in order to examine changes in grassland ecosystem behavior over the course of the main vegetation growth period in each case.

The results at Grillenburg showed, that the amount of rainfall received during our study period was well above the long-term annual mean (798 mm). Plant growth and biomass development only commenced in April, a time when PAR and temperature were favorable for plant growth. Mowing reduced LAI as well as biomass, with subsequent impact on overall assimilatory capacity of the grassland ecosystem. The pattern of root biomass development reflected seasonal variations in temperature and rainfall as well as the growth of the aboveground biomass with peak root mass being experienced between DOY 180 and 210, a time when soil temperature was highest. Peak belowground biomass accumulation coincided with reproductive stage, a time when plant assimilatory capacity was declining. Seasonal variation of leaf N concentration in the enclosure site showed a peak value at the beginning of the growing season. After flowering, N remained relatively constant until the end of the growing season. Cutting induced enhancement of aboveground N concentration, which came as a result of increased demand for N in the regenerating fresh tissue after the cut.

Seasonal pattern of CO_2 assimilation in this ecosystem are correlated with the observed pattern of biomass accumulation. During winter and early spring daily rates of net carbon exchange were low and the balance between NEE and respiration (R_{eco}) was nearly zero.

Immediately after harvesting, there is a period of approximately 2 weeks during which there is net emission of CO_2, but this changes to net uptake, when new tissues are formed. Unlike the mowed plots, the uncut locations despite having higher aboveground biomass, had lower GPP, likely the result of leaf aging and senescence as well as to partial shading by overlapping leaves.

Results from controlled experiments in the botanic gardens aimed to examine the impact of rainfall shifts showed that drought altered carbon fluxes in the grassland systems without significantly changing the aboveground biomass production. A possible consequence of drought in these grass species could be an increase in Leaf Area Index due to shifts in aboveground carbon allocation from reproductive to vegetative structures. The heavy rainfall manipulation resulted in no significant changes in NEE or above ground biomass production. The results showed a crucial role played by species composition in regulating carbon fluxes and ecosystem productivity. The more diverse community exhibited higher potential for carbon uptake as well as increased ecosystem respiration.

In Mediterranean grassland, daily maximum air temperatures increased steadily, with increased radiation input, from 11.6 °C in early March to 31.1 °C in late-May, while precipitation and soil moisture sharply decreased and most part of the vegetation withered in early-June. Trees, added considerable amounts of nutrients to the soil beneath their canopies, and had the potential to facilitate understory production. Although there was no significant difference in total biomass accumulation between understory and open locations, analysis of soil N concentration revealed higher soil N under the trees. Although NEE was limited by light intensity in the understory, model projection of GPP showed no difference between the understory and the open locations in their potential assimilatory capacities. Significant differences, however, occurred between the two locations in ecosystem respiration.

The results showed further that grazing increased foliar N concentration and decreased foliar C in the understory locations, with significant differences between the grazed and ungrazed sites. Root N and C concentrations declined in grazed locations in both the understory and open sites. However, there were no significant differences in soil N

concentration between grazed and ungrazed sites. Depending on the location under consideration (open vs understory), grazing influenced CO_2 exchange processes differently. We found no significant differences in GPP between grazed and ungrazed sites in the open locations, while large differences occurred in the understory, with lower NEE in the grazed as compared to the ungrazed locations.

Mean maximum aboveground foliar N concentration in the temperate grassland occurred in mid-May, coinciding with early growing season, with 3.4% nitrogen. In the Mediterranean grassland, foliar N concentration reached a peak value in early-April which was lower (2.3%) averaged over the stand biomass. As in the case of foliar N, root N concentration was also lower in the Mediterranean grassland (ca. 1 %) as compared to the temperate grassland (1.5%). In terms of available N in soil solution, it was low in Mitra (ca. 0.2 μmol g^{-1} soil) in early spring while it remained near 0.6 μmol g^{-1} soil throughout the season in Grillenburg. Thus, development of biomass is sensitive to fluctuations in temperature and PAR during the optimal period for growth, but the total biomass accumulation is at a lower level in the Portuguese grasslands (as well as the botanical garden communities) due to greater nutrient limitation. In general, the hypotheses (section 1.5) are supported by the studies that were carried out. Nevertheless, Mediterranean and temperate grasslands were found to differ more strongly than expected due to nutrient availability, which depends on the prevailing higher temperatures, annual changes in water balance and possibly nutrient removal from the ecosystem in Mediterranean regions. The results of the current study are viewed as very useful either to fill gaps in information or to provide a background concept for planning detailed experiments in grassland ecosystems of Iran**.**

Chapter 6
Deutsche Zusammenfassung

Gegenwärtige Prognosen deuten auf einen wahrscheinlichen Anstieg der globalen Temperatur um 1,1 bis 6,4 °C zwischen 1990 und 2100 aufgrund des Klimawandels. Die erwarteten Temperaturerhöhungen werden einem Anstieg der anthropogenen Treibhausgasemissionen zugeschrieben, welcher zu einer Erwärmung der Erdoberfläche und der unteren Atmosphäre durch eine Verstärkung des Treibhauseffektes führt. Um einen weiteren Anstieg des atmosphärischen CO_2-Spiegels zu verlangsamen ist es notwendig, dass Emissionen in die Atmosphäre signifikant reduziert werden und / oder dass die CO_2-Entnahme aus der Atmosphäre erhöht wird. Pflanzen spielen durch ihre Kohlenstoffsequestrierung eine wichtige Rolle in der globalen Kohlenstoffbilanz, indem sie der Atmosphäre CO_2 entziehen und durch Photosynthese, Translokation und Speicherung in Assimilate und Biomasse umwandeln.

Globale Schätzungen des relativen Anteils von Kohlenstoff in verschiedenen Ökosystemtypen besagen, dass Graslandökosysteme wahrscheinlich 10-30% des terrestrischen Kohlenstoffs speichern, und dass sie daher eine wichtige Rolle im Austausch von Treibhausgasen zwischen Biosphäre und Atmosphäre spielen. Temperate Grasländer stellen ungefähr 32 % der natürlichen Vegetation der Erde und etwa 20 % der Landfläche Europas. Mediterrane Ökosysteme bedecken zwar weniger als 5 % der Erdoberfläche, stellen jedoch etwa 20 % der weltweiten Flora, einschließlich wichtiger Komponenten in Grasländern.

In der vorliegenden Arbeit wurden die biophysikalischen Prozesse im Zusammenhang mit CO_2-Austausch, Biomasseproduktion sowie Nährstoffaufnahme und –nutzung in temperaten und mediterranen Graslandökosystemen vergleichend untersucht. Die Untersuchungen beschäftigen sich mit der Notwendigkeit, die Prozesse in Graslandökosystemen bezüglich Produktivität, Kohlenstoffaustausch und Nährstoffdynamik im Detail zu verstehen und wie diese Prozesse sich zu Umweltveränderungen und gegenwärtigen sowie zukünftigen Bewirtschaftungspraktiken verhalten. Ziel der Arbeit war es zu bestimmen, wie saisonale Änderungen in mikroklimatischen Bedingungen die Bodenwasser- und Nährstoffverfügbarkeit

beeinflussen und diese wiederum die Bioproduktivität von temperaten und mediterranen Grasländern verändern. Des weiteren wurde die Rolle der Heterogenität von Ökosystem, der Interaktionen von Arten und Bewirtschaftungspraktiken hinsichtlich CO_2- und Nährstoffaustausch mediterraner und temperater Grasländer untersucht.

Vor diesem Hintergrund wurden zwei Untersuchungsflächen in Mitteleuropa ausgewählt, zum einen ein bewirtschaftetes Grasland (Grillenburg), um den Einfluss der Mahd zu studieren, zum anderen eine für experimentelle Zwecke kontrolliert angelegte Graslandfläche (Botanischer Garten der Universität Bayreuth), um die Bedeutung normaler und extremer Wetterbedingungen auf Kohlenstoffaustausch, Produktivität und Nährstoffdynamik zu erfassen.

Auf den Experimentalflächen im Botanischen Garten wurde die Artendiversität variiert und die Effekte verschiedener Niederschlagsbehandlungen untersucht. Zusätzlich wurde eine anthropogene mediterrane Grasland-Savanne in Herdade da Mitra in Portugal beprobt, um den Einfluss von Klima, Bewirtschaftung (Beweidung) und Baumverteilung (Überschirmung oder Offenstand) auf die Funktion und Produktivität der krautigen Vegatation zu analysieren. Die Messungen des Netto-CO_2-Austauschs (NEE) wurden mittels geschlossenen Kammern durchgeführt. Die ober- und unterirdische Biomasse sowie Boden-Kohlenstoff- und Nährstoffpools wurden in denselben Plots beprobt. Die Messungen wurden periodisch durchgeführt, um Änderungen im Verhalten der verschiedenen Graslandökosysteme im Verlauf der Hauptvegetationsperiode verfolgen zu können.

Die Messungen zeigten, dass in Grillenburg während des Untersuchungszeitraumes die Niederschlagsmenge über dem langjährigen Mittel (798 mm) lag. Das Pflanzenwachstum und die Biomasseentwicklung begannen erst im April, als PAR und Temperatur günstig für das Pflanzenwachstum waren. Die Mahd reduzierte sowohl den LAI als auch die Biomasse mit einhergehendem Einfluss auf die Assimilationskapazität des Grasland-Ökosystems. Das Muster der Wurzelbiomasse-Entwicklung reflektierte die jahreszeitlichen Variationen in Temperatur und Niederschlag ebenso wie das Wachstum der oberirdischen Biomasse, mit Spitzenwurzelmasse zwischen Tag des Jahres 180 und 210, in einem Zeitraum, als die Bodentemperatur am höchsten war. Die Maxima der

unterirdischen Biomasseakkumulation fielen zusammen mit der reproduktiven Entwicklungsphase, zu einer Zeit, als die Pflanzenassimilationskapazität nachließ. Die saisonale Variation der Blattstickstoff-Konzentration in einer eingezäunten Kontrollfläche zeigte einen Maximalwert zu Beginn der Wachstumsperiode. Nach der Blüte blieb diese Konzentration bis zum Ende der Wachstumsperiode relativ konstant. Die Mahd induzierte eine Steigerung der oberirdischen Stickstoffkonzentration, durch den erhöhten Bedarf an Stickstoff im nachwachsenden Gewebe.

Saisonale Muster der CO_2-Assimilation in Grillenburg korrelieren mit den beobachteten Mustern der Biomasse-Akkumulation. Während des Winters und dem zeitigem Frühjahr waren die täglichen Raten des Netto-Kohlenstoffaustausches niedrig, und die Summe aus NEE und Ökosystematmung (Reco) war nahe Null. Unmittelbar an die Mahd schloss sich ein Zeitraum von ungefähr 2 Wochen an, in welchem es eine Netto-Emission von CO_2 gab; dieses änderte sich zur Nettoaufnahme, als neues Gewebe bildet wurde. Im Gegensatz zu den gemähten Flächen zeigten die ungemähten Stellen einen niedrigeren Brutto-CO_2-Aufnahme (GPP), obwohl sie eine höhere oberirdische Biomasse hatten. Letzteres war möglicherweise das Resultat von Blattalterung und Seneszenz als auch teilweiser Beschattung durch überlappende Blätter.

Die Ergebnisse der kontrollierten Experimente im Botanischen Garten, welche die Auswirkungen veränderter Niederschlagsregimes erforschen soll, zeigte, dass Trockenheit die Kohlenstoffflüsse in Graslandsystemen beeinflusst, ohne signifikante Änderung in der oberirdischen Biomasse-Produktion. Eine mögliche Konsequenz von Trockenheit in diesen Grasarten könnte eine Erhöhung des LAI wegen Verschiebungen in der oberirdischen Kohlenstoff-Allokation von reproduktiven zu vegetativen Organen sein. Künstlich erhöhter Niederschlag zeigte keine signifikanten Änderungen in NEE oder der Produktion oberirdischer Biomasse. Die Resultate verdeutlichen, dass die Artenzusammensetzung eine entscheidende Rolle bei der Regulation von Kohlenstoffflüssen und Ökosystemproduktivität spielt. Die Pflanzengemeinschaft mit höchster Biodiversität zeigte ein höheres Potenzial für Kohlenstoffaufnahme sowie auch eine erhöhte Ökosystem-Respiration.

Im mediterranen Grasland erhöhte sich die tägliche maximale Lufttemperatur mit zunehmendem Strahlungsangebot stetig, von 11,6 °C Anfang März bis 31,1 °C Ende Mai, während die Niederschläge und die Bodenfeuchte stark zurückgingen und der größte Teil der Vegetation Anfang Juni verwelkte. Die Bäume trugen beträchtliche Nährstoffmengen in den Boden unter ihren Kronen ein und haben so das Potenzial, die Unterwuchsproduktion zu begünstigen. Obwohl keine signifikanten Unterschiede zwischen Unterwuchs und Offenflächen bezüglich der Gesamtbiomasse-Akkumulation festzustellen waren, zeigten die Analysen der Bodenstickstoffkonzentration höhere Stickstoffgehalte unter den Bäumen.Obwohl NEE im Unterwuchs durch die Lichtintensität limitiert war, zeigte die Schätzung von GPP keinen Unterschied zwischen dem Unterwuchs und den Offenflächen in ihren potenziellen Assimilationskapazitäten. Signifikante Unterschiede gab es jedoch zwischen den beiden Standorten bezüglich der Ökosystematmung.

Die Resultate zeigten ferner, dass Beweidung die Blatt-Stickstoffkonzentration erhöhte und den Kohlenstoffgehalt der Blätter im Unterwuchs verringerte, mit signifikanten Unterschieden zwischen den beweideten und unbeweideten Flächen. Die Stickstoff- und Kohlenstoffkonzentrationen der Wurzeln nahmen auf beweideten Flächen ab, sowohl im Unterwuchs als auch auf Offenflächen. Es gab jedoch keine signifikanten Unterschiede der Bodenstickstoffkonzentration zwischen beweideten und unbeweideten Flächen. Es wurden keine signifikanten Unterschiede in GPP zwischen beweideten und unbeweideten Stellen in den offenen Flächen beobachtet, während es große Unterschiede unter Baumkronen mit niedrigerem NEE in den beweideten verglichen mit den unbeweideten Flächen gab.

Das durchschnittliche Maximum der Blatt-Stickstoffkonzentration wurde im Grasland der gemäßigten Zone mit 3,4 % Stickstoff Mitte Mai gefunden, während der frühen Wachstumsperiode. Im mediterranen Grasland erreichte die Blatt-Stickstoffkonzentration Maximalwerte Anfang April, welche über die Bestandesbiomasse gemittelt niedriger (2,3 %) waren als die der gemäßigten Zone. Wie im Falle des Blattstickstoffs war die Wurzelstickstoffkonzentration im mediterranen Grasland ebenfalls niedriger (ca. 1 %) im Vergleich zum temperaten Grasland (1.5%). Bezüglich des verfügbaren Stickstoffs in der Bodenlösung waren die Werte in Mitra im Frühjahr niedrig (ca. 0.2 μmol g^{-1} Boden)

während sie in Grillenburg über die gesamten Wachstumsperiode nahe 0,6 μmol g^{-1} Boden) blieben. Die Biomasse-Entwicklung reagiert demnach empfindlich auf Fluktuationen von Temperatur und PAR während der optimalen Wachstumsperiode. Die Gesamt- Biomasseakkumulation im portugisischen Grasland (ebenso wie in den Pflanzengemeinschaften des Botanischen Gartens) liegt jedoch wegen größerer Nährstofflimitierung auf niedrigerem Niveau.

Generell kann gesagt werden, dass die Ergebnisse der durchgeführten Studien die Hypothesen (Kapitel 1.5) unterstützen. Dennoch zeigte sich, dass die Grasländer der mediterranen und der gemäßigten Zone stärker als erwartet differieren, und zwar aufgrund der Nährstoff-Verfügbarkeit, welche abhängt von den höheren Temperaturen, dem saisonalen Wechsel der Wasserbilanz und dem Verlust von Nährstoffen aus dem Ökosystem in mediterranen Regionen. Die Resultate der vorliegenden Studie werden als sehr wertvoll zur Schließung von vorhandenen Wissenslücken erachtet. Gleichzeitig stellen sie auch ein Konzept für die Planung detaillierter Experimente in den Grasland-Ökosystemen des Iran dar.

Appendix

CO_2 gas exchange measurements with the Eddy covariance technique in Grillenburg

The eddy covariance technique was used to measure CO_2 flux in the temperate grassland in Grillenburg (Grünwald, unpublished). This site was established in March 2002. Half hourly measurements of CO_2 and H_2O fluxes, and microclimate parameters of air temperature, relative humidity, soil temperatures wind velocity and direction, precipitation, evaporation, latent heat, vapor pressure deficit and photosynthetically active radiation (PAR) are recorded (see Plate below). The following summary of methods and data processing was provided by Thomas Grünwald (Inst. Hydrology and Meteorology, Univ. Dresden) and Katherine Owen (Plant Ecology, UBT).

Plate A1. Eddy covariance and microclimate measurement tower at the Grillenburg meadow near Tharandt, Germany.

Eddy-covariance directly measures the net ecosystem exchange (NEE). The data can however, be split into Gross Primary Production (GPP) and the ecosystem respiration (*R*eco) using the general equation: GPP = R_{eco} − NEE (Baldocchi et al., 1996, 2001).

Ecosystem respiration was estimated from the nighttime CO_2 flux measurements. Low estimates of Reco, however, occur during conditions with low turbulent mixing (Grace *et al*.1996, Baldocchi *et al.* 2000, Paw *et al*. 2000, Aubinet *et al*. 2000). This under-estimation has to be corrected and it is usually done using the u* (friction velocity a measure of shear induced turbulence) corrections.

The nighttime CO_2 fluxes at air temperatures between 10 and 15 °C under well-watered conditions were related to friction velocity (*u**). These fluxes increased with *u** at low *u** and saturated at higher friction velocities. Based on a fitted function:

$\boldsymbol{F}c(u^*) = \boldsymbol{F}c\ max.(1 - e^{-ku^*})$

where:

Fc is the observed CO_2 flux, *u** the friction velocity, Fc_{max} the saturated *F*c (when *u** is not limiting), *k* the exponential parameter. At least 95% of the maximum nighttime CO_2 flux was reached at friction velocities above 0.2 m/s *(k* always >15 s/m). Consequently, all eddy-covariance data with *u** < 0.2 m/s were excluded from the analysis since it is likely that under these conditions, storage and advection can alter gas fluxes through the boundary layer.

Nighttime data criteria were taken as valid estimates of ecosystem respiration. Subsequently, for consecutive 14-day periods, a non-linear regression model according to Lloyd and Taylor (1994) was fitted to the observations of night-time ecosystem respiration (R_{eco}) versus air temperature (T_{air}) as follows:

$$R_{eco}(T_{air}) = R_{eco}(T_{ref}) \cdot e^{E_0\left(\frac{1}{T_{ref}-T_0}-\frac{1}{T_{air}-T_0}\right)}$$

where:

R_{eco} is ecosystem respiration, T_{ref} is 15 °C, T_0 is constant temperature (-46.02 °C) where respiration ceases, T_{air} is the air temperature and the free parameters are E_0, and R_{ref}, which E_0 is the activation energy-like parameter that determines the temperature sensitivity, and R_{ref} is the reference ecosystem respiration at 15°C. (cf. Reichstein et al. 2002, Subke et al. 2003).

R_{eco} *(*T_{ref}) is the estimated respiration at reference temperature (T_{ref}), In accordance with previous studies T_{ref} and T_0 were fixed at 10 and -46.02 °C, respectively (cf. Lloyd & Taylor, 1994), and allowed E_0 and R_{eco} *(*T_{ref}) to vary. Due to noise in the eddy-covariance data, the parameters could not be estimated for all the periods. If the standard error of the parameter estimate was larger than a heuristic threshold of 30% of the estimate the estimation was rejected, and the parameters were interpolated linearly from the last and the next valid 14-day period. The ecosystem respiration was then estimated from the half-hourly air temperature (day and night) according to the regression equation of each 14-day period (Adiku et al. 2005).

Gap filling of the meteorological and flux data was achieved by the marginal distribution sampling (cf. Reichstein et al. 2005, Owen et al. 2007). After the half-hourly database was prepared, daily, monthly and seasonal changes in NEE, GPP, and R_{eco} for the Grillenburg site during 2004 were calculated.

The results were provided by Thomas Grünwald, Institute of Hydrology and Meteorology, University of Dresden; they were compared to harvest measurements and chamber experiments carried out as part of this thesis.

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Erklärung

Hiermit erkläre ich, die vorliegende Arbeit selbständig verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt zu haben. Ich erkläre weiterhin weder diese noch eine gleichartige Doktorprüfung an einer anderen Hochschule endgültig nicht bestanden zu haben.

Heydar Mirzaei